RUN TO THE HILLS – PARTIAL MIGRATION IN LARGE HERBIVORES

By

WIBKE ERIKA BRIGITTA PETERS

B.Sc. International Forest Ecosystem Management, University of Applied Sciences Eberswalde, Germany, 2006
M.S. Wildlife Biology, University of Montana, Missoula, MT, USA, 2011

Dissertation

presented in partial fulfillment of the requirements
for the degree of

Doctor of Philosophy
in Fish and Wildlife Biology

The University of Montana
Missoula, MT

December 2015

Approved by:

Sandy Ross, Dean of The Graduate School
Graduate School

Dr. Mark Hebblewhite, Chair
Dept. of Ecosystem and Conservation Science, Wildlife Biology Program, University of Montana, USA

Dr. Francesca Cagnacci, Co-Chair
Dept. Biodiversity and Molecular Ecology, Fondazione Edmund Mach, Italy

Dr. Joel Berger
Dept. of Fish, Wildlife and Conservation Biology, Warner College of Natural Resources, Colorado State University, USA

Dr. Scott L. Mills
Dept. of Forestry and Environmental Resources, College of Natural Resources, North Carolina State University, USA

Dr. Atle Mysterud
Dept. of Biosciences, Centre for Ecological and Evolutionary Synthesis, University of Oslo, Norway

Peters, Wibke, PhD, fall 2015 *Fish and Wildlife Biology*

Run to the Hills – Partial Migration in Large Herbivores

Chairperson: Dr. Mark Hebblewhite

Co-Chairperson: Dr. Francesca Cagnacci

ABSTRACT

Partially migratory populations in which some individuals move to allopatric ranges during one season while others remain on their shared range, offer a unique opportunity to understand which factors shape the realized niche of individuals with plastic movement behaviors. For ungulates, forage and its spatiotemporal variability, risk (predation, humans) and density have been suggested to be the main determinants for the probability, distance and timing of migration. Roe deer (*Capreolus caproelus*), a small browsing ungulate with a high ecological plasticity and a wide distribution, present an ideal model species to test hypotheses on migration plasticity.

The green wave hypothesis predicts that migratory ungulates follow high quality forage, but has not been tested for browsers. I tested for differences in broad-scale vegetation composition and small-scale plant phenology and diet quality (using fecal nitrogen as a proxy) between resident (N=26) and migrant (N=11) roe deer in a diverse alpine study area in Northern Italy. Migrant and resident ranges differed at broader scales, phenology was similar and diet quality was significantly higher for migrants. I conclude that roe deer are selective for forage at different spatiotemporal scales and that the green- wave hypothesis may not be the only explanation for their migratory plasticity.

Therefore, I expanded from this single-population feeding niche comparison to testing if roe deer (N=71) switch or follow seasonal niches in five populations spanning wide resource gradients across Europe. I applied a novel integrative approach to classify/describe migration and assessed the determinants for niche differences between seasonal strategies. I found that migrants switched niches between winter and summer and the main niche differences were a function of topography, winter severity, spatiotemporal forage variation and density.

Lastly, I scaled up to a between-species comparison of roe and red deer (*Cervus elaphus*; N >500) to test hypotheses between and within species across a similar latitudinal gradient. Red deer had a much higher probability of migration with pronounced sex differences in contrast to the much less dimorphic roe deer. My results on the determinants driving plasticity in probability, distance and timing of migration, confirm the overall hypothesis that migration behavior is multi-causal and shaped by species' specific characteristics, including sexual dimorphism, feeding and breeding behavior.

ACKNOWLEDGEMENTS

Project and personal funding for this research was provided by the Fondazione Edmund Mach, Italy, the University of Montana, the National Aeronautics Space Agency (NASA) grant NNX11AO47G, Vectronic Aerospace, the George and Mildred Circia Scholarship and the International Research School in Applied Ecology, Norway.

I would like to thank my advisers Mark Hebblewhite and Francesca Cagnacci for the manifold support they have provided during the past four years. Their guidance and friendship greatly helped me to overcome many obstacles. I am immensely thankful for Mark Hebblewhite's kind patience, advice and teaching me to think big. Mark, you have been an inspiration and fabulous supervisor. I feel very fortunate having been able to learn from you during the past decade. I will always be indebted to Francesca Cagnacci's incredible dedication, passion and persistence that were instrumental in all stages of this project. Fran, thank you for your generosity, help and keeping me 'in orbita' over the past years. I am also immensely thankful to the rest of my academic research committee. It's been an absolute pleasure to work with Joel Berger, who always offered thoughtful expertise, has been an inspiration and added calm to turmoil even from the most remote field sites. From my first semester as a MS student at UofM, Scott Mills continues to amaze and inspire me as a role model, teacher and biologist. I owe a great deal of thanks Atle Mysterud who has been unfailingly available, efficient, and reminded me to ask the right questions. At the University of Montana, thanks to Jeanne Franz and Robin Hamilton for keeping me on track. This work would not have happened without their administrative support. Thanks to Robert Logan for backing up our data continuously, allowing graduate students to sleep better.

Much of the data that went into this Dissertation were the result of a thoughtful collaborative project, Eurodeer. It is a great honor to work with such broad-scale data and to be able to work with the biologists that were responsible for their collection. I am indebted to all Eurodeer members for providing data and offering most valuable advice. In particular, I want to thank Ferdinando Urbano for his enormous patience and offering help in a very timely manner. Most of my spatial analyses were made possible only through his expert assistance and data management. I owe thanks to Stefano Focardi who has been incredibly helpful with data analysis. Collection of empirical data in Trentino would not have been possible without logistical, administrative and technical support from the Parco Adamello-Brenta, Servizio Foreste e Fauna die Trentino, the Game wardens, the Trentino Hunting Association (ACT). I also want to thank the hunters without whom my field work in Chapter 2 would not have been possible.

This Dissertation work would not have been possible without the contribution of my many colleagues and fellow students, who also made this an exciting time. I benefited greatly from knowing exceptional people in the Hebblewhite lab including past and present members. During this PhD, especially Derek Spitz and Daniel Eacker offered generous help with data analysis and management. Mark Hurley always had great advice for getting the job done and challenged me to think critically. Thanks to Robin Steenweg for his incredibly positive philosophy. Joe St. Peter's help was instrumental during the last phase of my PhD. Thanks to Hugh Robinson for his wonderful sarcasm that generally put smile on my face. I would also like to thank the entire community of graduate

students for shaping this Wildlife Biology program. I am especially thankful to Josh Nowak for being a programming genius and generously providing help and a great deal of patience. Cindy, Jean and other victims of the writing process over the years - thanks for reviewing and commenting on my work.

I am indebted to the Cagnacci lab for their help in shaping this work and making my time in Italy so memorable. I shared wonderful times in the field with Maria Valent, Paola Semenzato, Sara Mancinelli, Simona Picardi, Valentina Zini, Filippo Bianchini, Deborah Capraro, Matteo Rizzuto and Miriam Wippler. I owe thanks to these amazing people for their incredible friendship and tireless efforts in the field making our work so much fun. I thank Federico Ossi for walking this PhD student path together and finding the right words of encouragement and availability to help when needed. Nathan Ranc made it easier for me to laugh at my mistakes and he generously helped to fix them. Johannes DeGroeve offered enormous patience with my data management attempts and just finished the job when he lost patience. Marco Ballardini was incredibly helpful processing samples. Thanks to Sandro Nicoloso, il tasso, for his humor, expertise and safely capturing roe deer. I thank the FEM FiRST PhD School staff, especially Alessandro Gretter and Flavia Zanon, and Heidi Hauffe, Annapaola Rizzoli, Marisa Caset and Giorgio Tonazzolli for administrative and logistical support.

Thanks to all my friends in Missoula, Trentino, at home and beyond for enriching all aspects of life, being there when needed, for the hugs, the treats and kind words. I am grateful to my Missoula support network for helping to minimize the emotional fluctuations of the last few years. I have been able to lean on Julie, Nicole, Molly, Tottie, Byron, Cindy and Clay. Thanks especially to Mary for always making me feel at home. Joe A., I am indebted to your humor, kindness and encouragement during the final push. Thanks to Jean for continuously helping me out and having an open ear when badly needed. In Trentino, Maurizio, Luisa B., Irene, Umberto and Luisa M. offered all sorts of advice and wonderful friendship. Thanks to kind long-term friends Nina, Julia and Sabrina for always being there for me! I would like to thank Florian Noll for being my cheerleader and genuine companion for most of this journey.

I am enormously grateful to my parents, Kerstin and Christian Peters, for their endless support, advocacy and encouragement of my ‘wild’ goals. I will never be able to thank my „drei Maedelchens” enough for their unwavering love and putting up with my moods. (Ihr wart immer mein Hafen. Prost!).

Finally, to the wild creatures - thanks for holding so many surprises and secrets that spark my curiosity.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1. INTRODUCTION AND OVERVIEW

Understanding what factors determine movement behavior has been the focus of much theoretical and empirical research in ecology. Animal movement can be defined as shifts in spatial locations in time and occur often in response to environmental variation (Senft et al. 1987, Wiens 1989, Nathan et al. 2008, Hebblewhite and Merrill 2009). The scale at which movements are undertaken varies (Ward and Saltz 1994). For example, fine scale movements can occur during daily activities in response to depletion of forage patches. At larger scales, long-distance migration may occur especially in seasonal environments (Zollner and Lima 1999, Taylor and Norris 2007). Consequently, movement is the behavioral mechanism that links the multi-scale process of resource selection (Johnson 1980). Due to the large spectrum of spatiotemporal resource variability, movement behaviors can take on many different forms (Dingle and Drake 2007, Hebblewhite and Merrill 2009, Cagnacci et al. 2011).

Migration is a widespread movement type and is classically defined as the seasonal movement of individuals from one region to another in response to changes in resources throughout space and time (Southwood 1962, Fryxell and Sinclair 1988, Dingle and Drake 2007). Due to the high scale-dependent spatiotemporal variability in resources, also migratory movements can range from local-scale altitudinal up- or downward movements with changing seasons (Igota et al. 2004, Boyle 2008), to long-distance migrations covering up to thousand kilometer stretches (Cox 2010). Consequently, this phenomenon affects distribution and abundance of animal populations (Dingle and Drake 2007). A large proportion of the world's taxa

undertake migratory movements at some stage in their lifecycle (Bauer and Hoye 2014). For example, approximately 20% of the world's bird species undergo some form of seasonal movement, spanning every continent and most landscapes (Cox 2010). Of all bat species about 30% are estimated to be long distance migrants, as well as 36% of marine mammals, all species of sea turtles and about 1% of terrestrial mammals (Robinson et al. 2009). However, these proportions are likely underestimates due to the diversity of migratory movement patterns (Dingle and Drake 2007).

While migration in general is assumed to increase fitness (Dingle and Drake 2007), ungulate migration in particular is considered an adaptive strategy to maximize fitness in seasonal environments through trade-offs between forage quality and predation risk (Fryxell et al. 1988, Bolger et al. 2008, Hebblewhite and Merrill 2009). Landscapes that show very little variation should support sedentary populations, while landscapes that vary across broad scales, but are predictable should favor migration (Jonzén et al. 2011, Mueller et al. 2011, Hein et al. 2012). Previous studies often treated ungulate migration as a fixed and discrete phenomenon of clear migrant versus resident behavior. However, today it is becoming more evident that ungulate migration is very flexible and most ungulates display a behavioral plasticity of migration 'tendency' in response to favorable conditions or stochastic events (Cagnacci et al. 2011, Cresswell et al. 2011, Mysterud et al. 2011, Sih et al. 2012). One example of this behavioral plasticity is exemplified by partial migration.

Partial migration occurs when only a fraction of the population migrates and another remains resident either in the breeding or non-breeding range (Dingle and

Drake 2007, Skov et al. 2011, Singh et al. 2012). Interestingly, many migratory ungulates are partially migratory, such as impala (*Aepyceros melampus;* Gaidet and Lecomte 2013), roe deer (*Capreolus capreolus*; Cagnacci et al. 2011, Peters et al. in prep [Chapter 2], Peters et al. in prep [Chapter 3], Peters et al. in prep [Chapter 4]), Serengeti wildebeest (*Connochaetes taurinus*; Fryxell et al. 1988), moose (*Alces alces*; Ball et al. 2001), sika deer (*Cervus nippon yesoensis*; Igota et al. 2004), pronghorn (*Antilocapra americana*, White et al. 2007), red deer (*Cervus elaphus elaphus*; Mysterud et al. 2011, Peters et al. in prep [Chapter 4]), elk (*Cervus elaphus canadensis*; Hebblewhite et al. 2008), white-tailed deer (*Odocoileus virginianus*; Grovenburg et al. 2011), or reindeer (*Rangifer tarandus*; Hansen et al. 2010). Little is known about determinants of migratory behavioral flexibility in ungulates, however, despite the key role they play in ecosystems (Gordon et al. 2004). Understanding the determinates of migration is sorely needed to understanding adaptation to environmental changes (Bolger et al. 2008). Recent research shows declines in migration in partially migratory ungulates following human development, recolonizing predators, and potentially climate change (Berger 2004, Hebblewhite et al. 2006, Middleton et al. 2013). Although partial migration is the most common form of migration, it remains relatively unstudied (Chapman et al. 2011a).

Behavior in a partially migratory population can vary along a gradient from residency to migration within individuals (Dingle and Drake 2007). In particular, individuals can show variation in migratory behavior from year to year due to condition dependence in a facultative manner (Nelson 1995, Fieberg et al. 2008, Grovenburg et al. 2011). The proportion of migrants within a population commonly

depends on the quality of the breeding or non-breeding range, relative densities on the breeding and non-breeding range (Lundberg 1988, Taylor and Norris 2007) and the energetic or settlement costs of migration (Alexander 1998, Cresswell et al. 2011). Also, predictability of spatial and temporal heterogeneity of resources are key factors to affect the portion of migrating animals in a population (Sinclair 1983, Holdo et al. 2009, Jonzén et al. 2011, Mueller et al. 2011).

Based on ecological niche theory different species can only thrive within certain ranges of environmental conditions (Hutchinson 1957). Plasticity of migratory behavior may be an important component of an individual's life history and ecological niche (Morin and Lechowicz 2008). Niche variation allows individuals within populations to occupy a subset of the species' environmental niche given resource heterogeneity, which affords different life-history opportunities to survive and reproduce (Van Valen 1965, Bolnick et al. 2003, Araujo et al. 2011, Chapman et al. 2011b). Thus, the drivers of plasticity in partially migratory populations may be species' specific and migratory plasticity is likely best explained as complex adaptive behavioral gradient in response to abiotic and biotic resources that comprise the environmental niche of a species, population and individual. Consequently, linking space-time data of limiting resources to seasonal movements is the key to understanding ecological plasticity in migratory behavior (Pulliam 2000, Jonzén et al. 2011). This complexity necessitates a multi-scale and comparative multi-species approach.

Herein, I present a sequence of chapters that are embedded under the greater theme of investigating partial migration in ungulates. To address different key

questions on migration plasticity I structured my Dissertation into three main sections, each of which explores different themes of partial migration at different spatiotemporal scales. This hierarchical structure allowed me to describe and assess factors affecting partial migration from the level of the individual within a single study area to between population comparisons across a continental scale, and finally a between-species comparison. I use roe deer global positioning system (GPS) collar data in all three sections. Roe deer are suitable for the study of partial migration due to their high degree of behavioral plasticity. The European roe deer is a small ungulate (20-30 kg; Andersen et al. 1998) and amongst the most common ungulate species in Europe (Melis et al. 2009). Roe deer occupy a wide range of habitats from northern Scandinavian boreal forest to Mediterranean chaparral environments (Andersen et al. 1998). At the latitudinal and altitudinal extremes of its distribution range, diverse habitat selection patterns including seasonal migration, allow roe deer to adapt to changes in habitat suitability in space and time (Mysterud 1999, Ramanzin et al. 2007, Cagnacci et al. 2011). Roe deer display a high level of behavioral plasticity (Cagnacci et al. 2011). As a pure browser (Hofmann 1973, Van Soest 1994) roe deer are able to forage on a very wide range of high quality plants, but have a strong seasonal diet specialization (Duncan et al. 1998, Cornelis et al. 1999).

DISSERTATION OUTLINE

Broadly, my Dissertation has the following structure: At the smallest spatiotemporal scale I use GPS data of roe deer from a partially migratory population in one mountainous study area in Italy to test for differences in forage quality and plant composition and phenology between resident and migrant roe deer in my second

chapter. While there have been several studies relating forage to seasonal movements for grazers and mixed feeders (Hebblewhite et al. 2008), to my knowledge this study provides one of the first examples addressing forage benefits of migration in a small browser. Next, environmental conditions vary in space, fluctuate over time and essentially define what areas can be inhabited by organisms at any given time (Jonzén et al. 2011). In my third chapter I expand to a between population comparison of partial migration and seasonal niches in roe deer across five different European populations using GPS data of 71 roe deer to explain variation in migratory plasticity at intra- and inter-population levels. While these two chapters reveal important insights into the multi-facetted determinants of roe deer migration ecology, in my last chapter I expanded my scope to a between-species comparison of a browser (roe deer) and a mixed feeder (red deer). I assess differences and similarities in migratory traits and explain determinants thereof using a unique and very large dataset of > 500 roe and red deer individuals across Europe.

RELATING FORAGE TO SEASONAL MOVEMENTS OF A SMALL UNGULATE BROWSER IN THE ITALIAN DOLOMITES

The green-wave hypothesis (Owen 1980) predicts that migratory herbivores should follow gradients of forage green-up. Because of lower temperatures and increased snow depths at higher elevations, altitudinal migration may yield benefits in terms of increased access to newly emergent forage of higher quality forage throughout the growing season (Hebblewhite et al. 2008, Bischof et al. 2012). While this hypothesized link between forage phenology and migration has been tested for grazers (Holdo et al. 2009) and mixed feeders (Hebblewhite et al. 2008, Bischof et al.

2012), the relationship remains largely untested for browsers. In fact, it has been suggested that for browsers, such as roe deer, high population densities on winter ranges may affect the probability of migration rather than phenological gradients (Mysterud et al. 2012). In chapter two, I tested if migratory browsers follow phenological gradients and have access to higher diet quality than resident individuals. I used fine-scale empirical data on vegetation phenology gradients and diet quality based on fecal nitrogen (FN) indices (Leslie et al. 2008) along movement trajectories of 22 roe deer sampled across two years (36 total sampling years) in a very diverse mountainous study area in northern Italy. I found that while roe deer migrants and residents inhabited very different broad scale vegetation types throughout the summer, finer scale plant phenology did not differ between seasonal movement strategies. However, migratory roe deer consistently had higher diet quality using two different measures of FN throughout the vegetation season. Consequently, my results indicate that forage selectivity differed between resident and migrant roe deer, but likely at various spatiotemporal scales. This finding underlines the hierarchical nature of animal movement (Nathan et al. 2008), habitat selection (Johnson 1980) and particularly foraging behavior (Senft et al. 1987).

In the same study area working together with a M.S. student on the manuscript Mancinelli et al. (*in revision;* Appendix 1) we show that roe deer habitat selection is a multi-scale process across different gradients of time and space. Our results from resource selection functions (RSF; Boyce et al. 2002) suggested that despite a high ecological plasticity with respect to broad-scale habitat variables, roe deer were selective for finer-scale habitat characteristics, such as the availability of high-quality

forage. This result combined with my findings in the second chapter suggest that roe deer migrants switched broad seasonal realized niches between winter and summer ranges and were able to obtain higher quality forage in higher elevation habitat types. Yet, resident individuals had access to similar phenological gradients, but were not able to achieve the same forage quality, potentially due to overall lower diet quality species in their lower elevation ranges. Consequently, because fine-scale forage gradients did not seem to paint a conclusive picture to explain the migratory behavior, but rather may be just one factor contributing to migration in this small browser, I next tested multiple hypotheses regarding the role of combined abiotic and biotic multi-causal factors in shaping migratory plasticity in roe deer.

MIGRATION ACROSS THE HUTCHINSONIAN NICHE IN SPACE AND TIME BY A LARGE HERBIVORE

In chapter three, I scaled up from small scale feeding behavior between resident and migrant roe deer and applied niche theory to both describe the process of migration and assess determinants (i.e. the mechanisms) of the phenomenon in roe deer. To assess which factors determine migration, first the process of migration has to be described and individuals classified into different seasonal movement types. This classification is a much debated topic in the study of migration (Cagnacci et al. *in revision*). Migration is commonly defined by the spatial separation of seasonal ranges and its classification is often solely based on Cartesian descriptive measures. Migration across far horizontal distances is probably the best known form of migration (Dingle and Drake 2007). However, due to the high plasticity in migratory movements (Cagnacci et al. 2011), migration may occur in a number of ways. Besides

long-distance migrations, also upward or downward altitudinal movements with relatively short horizontal distances (Igota et al. 2004) or migrations across ecological distances between different seasonal niches have been described (LeResche 1974). Because the underlying mechanism for migration is hypothesized to occur in response to spatiotemporal resource variability and the ecological niche of as species is dynamic, it seems intuitive to describe migration as shifts in seasonal niches (Laube et al. 2015). This concept has been tested for birds and some avian species switch their seasonal niches, while others track them throughout the year (Nakazawa et al. 2004). However, especially for ungulates it is not well understood if migrants move to a different ecological niche or if they track similar niches year-round (Laube et al. 2015).

I considered both of these concepts, the geographic space and the environmental niche space, to test the utility of an integrative approach to classify, or describe, migratory behavior using geographic and environmental distance measures. I used GPS data of 71 roe deer in five populations spanning a wide latitudinal gradient across the European continent. These data represent a subset of the data used in the following chapter (chapter four) and include individuals from populations which have been shown to be partially migratory with high proportions of migrants as well as one population dominated by resident individuals (Appendix 3-A; Cagnacci et al. 2011) to allow comparisons between residents and migrants. I first assessed if roe deer followed or switched realized ecological niches when migrating by quantifying the ecological distance between seasonal ranges based on multivariate analyses (Doledec and Chessel 1987) and the seasonal niche overlap using Schoener's *D* (Schoener

1974). I found that roe deer migrate in geographic as well as environmental space. I then combined classification measures derived in geographic and ecological space for an integrative classification of roe deer migration behavior. This integrative approach returned a parsimonious classification of resident (N=53) and migrant (N=18) roe deer. Next, I tested which environmental covariates determined these behavioral differences in seasonal movements using discriminant analysis and generalized linear models at the scale of the individual and population.

My results indicated that at the individual level, migration was a function of forage, topography and risk factors. At the population level, migration was strongly driven by density as well as spatial variation of seasonal forage resources. In chapters two and three, I found some support for forage affecting migration, while chapter three also revealed several other factors, density being one of the main ones. This supports the competition avoidance hypothesis that predicts that migration probability increases if migrants have access to summer ranges with lower densities (Mysterud et al. 2011, Mysterud et al. 2012). Future research should focus on how potentially interacting effects between density and forage affect migration probability in roe deer. Further, the fitness consequences of niche switching versus niche following (Pulliam 2000) remains to be tested.

Assessing Determinants of Migratory Behavior for Two Large Herbivores with Contrasting Species-Specific Traits

Because my third chapter revealed pronounced differences in migration behavior between populations of roe deer spanning a wide latitudinal gradient, I next addressed different hypotheses to understand if such differences also emerge when comparing

different ungulates with contrasting species-specific traits. Therefore, in my last chapter (chapter four) I used a very large GPS dataset of more than 500 sampling years spanning of 10 roe deer and 12 red deer populations across a similar latitudinal gradient, including a greater span of roe deer populations than used in my third chapter. I first tested for differences in migration probability, distance and timing between species. Next, I tested hypotheses addressing the factors that determine differences in each of these response variables within each species. To address hypotheses on migration plasticity between these species, I combined GPS data with broad-scale Global Information System (GIS) data to describe gradients in topography, climate and spatiotemporal resource variability.

My main findings are that migration probability was overall much higher in red deer than in roe deer. Of 264 red deer observations more than 50% were classified as migratory, with a much higher proportion in males than females. In contrast of 273 roe deer only about 20% were migratory with no sex-specific differences. Also, I found significant differences in the timing and distance of migration that suggested that the determinants for migration behavior are multi-causal in these different ungulate species as already found in chapter three for roe deer. For example, the differences in the probability of migration between sexes may be attributed to the low sexual size dimorphism of roe deer compared to red deer. Trade-offs of migration may be more similar for roe deer of both sexes (Cagnacci et al. 2011) compared to dimorphic red deer (Kie and Bowyer 1999, Bowyer 2004). This hypothesis is also supported by the fact the migration timing in spring did not differ between sexes in roe deer, but differed in red deer. As an income breeder, roe deer males may be able

to obtain higher quality forage to maintain territories prior to the rut while female roe deer may be able to obtain important resources prior to giving birth and during lactation (Vanpé et al. 2010). Supporting this hypothesis I found no statistically significant differences in diet quality between sexes in Chapter 2. My results also revealed important general mechanisms that affect migration behavior across species. For example, migration probability was a function of limiting winter conditions at northern latitudes and higher elevations for both species, suggesting that these factors are important determinants for migration behavior across ungulates. This result is supported by many studies on different ungulate species at northern latitudes including mule deer, moose and white tailed deer (Nicholson et al. 1997, Ball et al. 2001, Sabine et al. 2002). Lastly, while I was able to address the effect of density on migration probability in chapter three, these data were not available across all population of red and roe deer in chapter four. Therefore, I again suggest that future research may focus on density-dependent (Fryxell and Sinclair 1988) effects on migration behavior in different species sharing similar distribution ranges.

Overall, results from my dissertation aid to understand determinants of migratory plasticity in ungulates from the individual level to the level of different species. I tested the effectiveness of various approaches to reach a definition for partial migration and address variability of several migratory traits, such as timing, distance or duration of migration. Achieving these results was only feasible using animal movement data of multiple populations and species. My large scale analyses in chapters three and four were only possible with data from the Eurodeer project (www.eurodeer.org).

DISSERTATION FORMAT

The following chapters are intended for publication in specific peer-reviewed scientific journals. The intended journal is given as footnote in the title for each chapter. As each of these chapters reflects not just the work of myself, but that of many important collaborators (see Acknowledgements), I use the collective "we" throughout my Dissertation. Appendix 1 is a manuscript by a MS student within the empirical field project in Trentino, Italy (chapter two) I co-authored.

LITERATURE CITED

Alexander, R. M. 1998. When is migration worthwhile for animals that walk, swim or fly? Journal of Avian Biology **29**:387-394.

Andersen, R., P. Duncan, and J. D. C. Linnell. 1998. The European roe deer: the biology of success. Scandinavian University Press, Oslo.

Araujo, M. S., D. I. Bolnick, and C. A. Layman. 2011. The ecological causes of individual specialisation. Ecology Letters **14**:948-958.

Ball, J. P., C. Nordengren, and K. Wallin. 2001. Partial migration by large ungulates: characteristics of seasonal moose *Alces alces* ranges in northern Sweden. Wildlife Biology **7**:39-47.

Bauer, S. and B. J. Hoye. 2014. Migratory Animals Couple Biodiversity and Ecosystem Functioning Worldwide. Science **344**.

Berger, J. 2004. The last mile: How to sustain long-distance migration in mammals. Conservation Biology **18**:320-331.

Bischof, R., L. E. Loe, E. L. Meisingset, B. Zimmermann, B. Van Moorter, and A. Mysterud. 2012. A Migratory Northern Ungulate in the Pursuit of Spring: Jumping or Surfing the Green Wave? American Naturalist **180**:407-424.

Bolger, D. T., W. D. Newmark, T. A. Morrison, and D. F. Doak. 2008. The need for integrative approaches to understand and conserve migratory ungulates. Ecology Letters **11**:63-77.

Bolnick, D. I., R. Svanback, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. A. Forrister. 2003. Comparative approaches to intra-population niche variation. Integrative and Comparative Biology **43**:1078-1078.

Bowyer, R. T. 2004. Sexual Segregation in Ruminants: Definitions, Hypotheses, and Implications for Conservation and Management.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling **157**:281-300.

Boyle, W. A. 2008. Partial migration in birds: tests of three hypotheses in a tropical lekking frugivore. Journal of Animal Ecology **77**:1122-1128.

Cagnacci, F., S. Focardi, A. Ghisla, B. Van Moorter, E. Gurarie, M. Heurich, A. Mysterud, J. Linnell, M. Panzacchi, and M. Roel. in revision. How many routes lead to migration? Re-establishing the link between definitions, methods and movemet ecology. Journal of Animal Ecology.

Cagnacci, F., S. Focardi, M. Heurich, A. Stache, A. J. M. Hewison, N. Morellet, P. Kjellander, J. D. C. Linnell, A. Mysterud, M. Neteler, L. Delucchi, F. Ossi, and F. Urbano. 2011. Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. Oikos **120**:1790-1802.

Chapman, B. B., C. Brönmark, J.-Å. Nilsson, and L.-A. Hansson. 2011a. The ecology and evolution of partial migration. Oikos **120**:1764-1775.

Chapman, B. B., K. Hulthen, D. R. Blomqvist, L. A. Hansson, J. A. Nilsson, J. Brodersen, P. A. Nilsson, C. Skov, and C. Bronmark. 2011b. To boldly go: individual differences in boldness influence migratory tendency. Ecology Letters **14**:871-876.

Cornelis, J., J. Casaer, and M. Hermy. 1999. Impact of season, habitat and research techniques on diet composition of roe deer (Capreolus capreolus): a review. Journal of Zoology **248**:195-207.

Cox, G. W. 2010. Bird Migration and Global Change. Island Press.

Cresswell, K. A., W. H. Satterthwaite, and G. A. Sword. 2011. Understanding the evolution of migration through empirical examples. Pages 7-16 *in* E. J. Milner-Gulland, J. Fryxell, and A. R. E. Sinclair, editors. Animal migration: A synthesis Oxford University Press, New York, NY.

Dingle, H. and V. A. Drake. 2007. What is migration? Bioscience **57**:113-121.

Doledec, S. and D. Chessel. 1987. Rythmes saisonniers et composantes stationnelles en milieu aquatique. I. Description d'un plan d'observations complet par projection de variables. Acta Oecologica, Oecologia Generalis **8**:403-426.

Duncan, P., H. Tixier, R. R. Hofman, and M. Lechner-Doll. 1998. Feeding strategies and the physiology of digestion in roe deer. Pages 91-116 *in* R. Andersen, P. Duncan, and J. Linnell, editors. The European roe deer: the biology of success. Scandinavian University Press, Oslo.

Fieberg, J., D. W. Kuehn, and G. D. DelGiudice. 2008. Understanding Variation in Autumn Migration of Northern White-tailed Deer by Long-term Study. Journal of Mammalogy **89**:1529-1539.

Fryxell, J. M., J. Greever, and A. R. E. Sinclair. 1988. Why are ungulate so abundant. American Naturalist **131**:781-798.

Fryxell, J. M. and A. R. E. Sinclair. 1988. Causes and Consequences of Migration by Large Herbivores. Trends in Ecology & Evolution **3**:237-241.

Gaidet, N. and P. Lecomte. 2013. Benefits of migration in a partially-migratory tropical ungulate. BMC Ecology **13**.

Gordon, I. J., A. J. Hester, and M. Festa-Bianchet. 2004. REVIEW: The management of wild large herbivores to meet economic, conservation and environmental objectives. Journal of Applied Ecology **41**:1021-1031.

Grovenburg, T. W., C. N. Jacques, R. W. Klaver, C. S. DePerno, T. J. Brinkman, C. C. Swanson, and J. A. Jenks. 2011. Influence of landscape characteristics on migration strategies of white-tailed deer. Journal of Mammalogy **92**:534-543.

Hansen, B. B., R. Aanes, and B. E. Saether. 2010. Partial seasonal migration in high-arctic Svalbard reindeer (Rangifer tarandus platyrhynchus). Canadian Journal of Zoology-Revue Canadienne De Zoologie **88**:1202-1209.

Hebblewhite, M., E. Merrill, and G. McDermid. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. Ecological Monographs **78**:141-166.

Hebblewhite, M. and E. H. Merrill. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology **90**:3445-3454.

Hebblewhite, M., E. H. Merrill, L. E. Morgantini, C. A. White, J. R. Allen, E. Bruns, L. Thurston, and T. E. Hurd. 2006. Is the migratory behaviour of montane elk herds in peril? The case of Alberta's Ya Ha Tinda elk herd. Wildlife Society Bulletin **34**:1280-1295.

Hein, A. M., C. Hou, and J. F. Gillooly. 2012. Energetic and biomechanical constraints on animal migration distance. Ecology Letters **15**:105-110.

Hofmann, R. R. 1973. The ruminant stomach: stomach structure and feeding habits of East African game ruminants. . Pages pp. 1–364. *in* T. R. Odhiambo, editor. East African Monographs in Biology, vol. 2. East African Literature Bureau, Nairobi.

Holdo, R. M., R. D. Holt, and J. M. Fryxell. 2009. Opposing Rainfall and Plant Nutritional Gradients Best Explain the Wildebeest Migration in the Serengeti. American Naturalist **173**:431-445.

Hutchinson, G. E. 1957. Concluding remarks. Pages 415-427 *in* Cold Spring Harbour Symposium on Quantitative Biology

Igota, H., M. Sakuragi, H. Uno, K. Kaji, M. Kaneko, R. Akamatsu, and K. Maekawa. 2004. Seasonal migration patterns of female sika deer in eastern Hokkaido, Japan. Ecological Research **19**:169-178.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology **61**:65-71.

Jonzén, N., E. Knudsen, R. Holt, and B. Sæther. 2011. Uncertainty and predictability: the niches of migrants and nomads.*in* E. J. Milner-Gulland, J. Fryxell, and A. R. E. Sinclair, editors. Animal Migration: A Synthesis. Oxford University Press, Oxford.

Kie, J. G. and R. T. Bowyer. 1999. Sexual Segregation in White-Tailed Deer: Density-Dependent Changes in Use of Space, Habitat Selection, and Dietary Niche. Journal of Mammalogy **80**:1004-1020.

Laube, I., C. H. Graham, and K. Böhning-Gaese. 2015. Niche availability in space and time: migration in Sylvia warblers. Journal of Biogeography:n/a-n/a.

LeResche, R. E. 1974. Moose migrations in North America. Naturaliste Canadien **101**:393-415.

Leslie, D. M., R. T. Bowyer, and J. A. Jenks. 2008. Facts From Feces: Nitrogen Still Measures Up as a Nutritional Index for Mammalian Herbivores. Journal of Wildlife Management **72**:1420-1433.

Lundberg, P. 1988. The Evolution of Partial Migration in Birds. Trends in Ecology & Evolution **3**:172-175.

Mancinelli, S., W. Peters, L. Boitaini, M. Hebblewhite, and F. Cagnacci. in revision. Roe deer summer habitat selection at multiple spatio-temporal scales in an 1 Alpine environmen. Hystrix-Italian Journal of Mammalogy.

Melis, C., B. Jedrzejewska, M. Apollonio, K. A. Barton, W. Jedrzejewski, J. D. C. Linnell, I. Kojola, J. Kusak, M. Adamic, S. Ciuti, I. Delehan, I. Dykyy, K. Krapinec, L. Mattioli, A. Sagaydak, N. Samchuk, K. Schmidt, M. Shkvyrya, V. E. Sidorovich, B. Zawadzka, and S. Zhyla. 2009. Predation has a greater impact in less productive environments: variation in roe deer, Capreolus capreolus, population density across Europe. Global Ecology and Biogeography **18**:724-734.

Middleton, A. D., M. J. Kauffman, D. E. McWhirther, J. G. Cook, R. C. Cook, A. A. Nelson, M. D. Jimenez, and R. W. Klaver. 2013. Animal migration amid shifting patterns of phenology and predation: Lessons from a Yellowstone elk herd Ecology.

Morin, X. and M. J. Lechowicz. 2008. Contemporary perspectives on the niche that can improve models of species range shifts under climate change. Biology Letters **4**:573-576.

Mueller, T., K. A. Olson, G. Dressler, P. Leimgruber, T. K. Fuller, C. Nicolson, A. J. Novaro, M. J. Bolgeri, D. Wattles, S. DeStefano, J. M. Calabrese, and W. F. Fagan. 2011. How landscape dynamics link individual- to population-level movement patterns: a multispecies comparison of ungulate relocation data. Global Ecology and Biogeography **20**:683-694.

Mysterud, A. 1999. Seasonal migration pattern and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway. Journal of Zoology **247**:479-486.

Mysterud, A., R. Bischof, L. E. Loe, J. Odden, and J. Linnell. 2012. Contrasting migration tendencies of sympatric red deer and roe deer suggest multiple causes of migration in ungulates. Ecosphere **3:10, art92**.

Mysterud, A., L. E. Loe, B. Zimmerman, R. Bischof, V. Veiberg, and E. Meisingset. 2011. Partial migration in expanding red deer populations at northern latitudes – a role for density dependence? Oikos **120**:1817-1825.

Nakazawa, Y., A. T. Peterson, E. Martínez-Meyer, and A. G. Navarro-Sigüenza. 2004. Seasonal Niches of Nearctic-Neotropical Migratory Birds: Implications for the Evolution of Migration. The Auk **121**:610-618.

Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences of the United States of America **105**:19052-19059.

Nelson, M. E. 1995. Winter range arrival and departure of white-tailed deer in northeastern Minnesota. Canadian Journal of Zoology-Revue Canadienne De Zoologie **73**:1069-1076.

Nicholson, M. C., R. T. Bowyer, and J. G. Kie. 1997. Habitat selection and survival of mule deer: Tradeoffs associated with migration. Journal of Mammalogy **78**:483-504.

Owen, M. 1980. Wild geese of the world. Their Life and Ecology. B. T. Batsford Ltd. London.

Pulliam, H. R. 2000. On the relationship between niche and distribution. Ecology Letters **3**:349-361.

Ramanzin, M., E. Sturaro, and D. Zanon. 2007. Seasonal migration and home range of roe deer (Capreolus capreolus) in the Italian eastern Alps. Canadian Journal of Zoology-Revue Canadienne De Zoologie **85**:280-289.

Rousseeuw, P. J. 1987. Silhouettes: A graphical aid to the interpretation and validation of cluster analysis. Journal of Computational and Applied Mathematics **20**:53-65.

Sabine, D. L., S. F. Morrison, H. A. Whitlaw, W. B. Ballard, G. J. Forbes, and J. Bowman. 2002. Migration behavior of white-tailed deer under varying winter climate regimes in New Brunswick. Journal of Wildlife Management **66**:718-728.

Schick, R. S., S. R. Loarie, F. Colchero, B. D. Best, A. Boustany, D. A. Conde, P. N. Halpin, L. N. Joppa, C. M. McClellan, and J. S. Clark. 2008. Understanding movement data and movement processes: current and emerging directions. Ecology Letters **11**:1338-1350.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science **185**:27-39.

Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. Bioscience **37**:789-795 & 798-799.

Sih, A., J. Cote, M. Evans, S. Fogarty, and J. Pruitt. 2012. Ecological implications of behavioural syndromes. Ecology Letters **15**:278-289.

Sinclair, A. R. E. 1983. The function of distance movement in verterbrates. Pages 248-258 *in* I. R. Swingland and P. J. Greenwood, editors. The Ecology of Animal Movements. Claredon Press, Oxford.

Singh, N. J., L. Borger, H. Dettki, N. Bunnefeld, and G. Ercsson. 2012. From migration to nomadism: movemnet varaibility in a northern ungulate accross its latitudinal range. Ecological Applications **22**:2007-2020.

Skov, C., H. Baktoft, J. Brodersen, C. Bronmark, B. Chapman, L. A. Hansson, and P. A. Nilsson. 2011. Sizing up your enemy: individual predation vulnerability predicts migratory probability. Proceedings of the Royal Society B-Biological Sciences **278**:1414-1418.

Southwood, T. R. E. 1962. Migration of terrestrial arthropods in relation to habitat. Biological Reviews **37**:171-211.

Taylor, C. M. and D. R. Norris. 2007. Predicting conditions for migration: effects of density dependence and habitat quality. Biology Letters **3**:280-283.

Van Soest, P. J. 1994. Nutritional Ecology of the Ruminant. Cornell University, O & B Books Inc., NW Kline Place, USA.

Van Valen, L. 1965. Morphological variation and width of ecological niche. American Naturalist **99**:377-390.

Vanpé, C., J.-M. Gaillard, P. Kjellander, O. Liberg, D. Delorme, and A. J. M. Hewison. 2010. Assessing the intensity of sexual selection on male body mass and antler length in roe deer Capreolus capreolus: is bigger better in a weakly dimorphic species? Oikos **119**:1484-1492.

Ward, D. and D. Saltz. 1994. Foraging at Different Spatial Scales - Dorcas Gazelles Foraging for Lilies in the Negev Desert. Ecology **75**:48-58.

White, P. J., T. L. Davis, K. K. Barnowe-Meyer, R. L. Crabtree, and R. A. Garrott. 2007. Partial migration and philopatry of Yellowstone pronghorn. Biological Conservation **135**:502-510.

Wiens, J. A. 1989. Spatial Scaling in Ecology. Functional Ecology **3**:385-397.
Zollner, P. A. and S. L. Lima. 1999. Search strategies for landscape-level interpatch movements. Ecology **80**:1019-1030.

CHAPTER 2. RELATING FORAGE TO SEASONAL MOVEMENTS OF A SMALL UNGULATE BROWSER IN THE ITALIAN DOLOMITES[1]

INTRODUCTION

All animals search for, encounter and consume food, and foraging behavior is directly linked to animal fitness through body mass, reproductive success and survival (Mysterud et al. 2001b). Foragers from small insects (Avgar et al. 2008) to large wildebeest (*Connochaetes taurinus*; Wilmshurst et al. 1999) change their movements in response to forage availability and quality. Relationships between forage and their consumers are complex, particularly in herbivores, which feed on a wide range of plants (Barancekova et al. 2010). Therefore, characterizing herbivore diet and its spatiotemporal variation remains a challenging task (Pompanon et al. 2011). Plant species greatly vary in quality depending on growth type (Hebblewhite et al. 2008) and spatiotemporal variation in phenological development can extend the nutritional benefits of emerging plants (Fryxell et al. 1988). For example, abiotic factors, such as topography or snow, can lead to temporal variability in plant growth (Albon and Langvatn 1992). Consequently, spatial heterogeneity resulting from temporal variation leads to nutritional variability and prolongs the availability of nutritious plants (Fryxell et al. 2005, Pettorelli et al. 2007).

The green-wave hypothesis (Owen 1980) suggests that herbivores should follow phenological gradients to optimize access to high-quality forage for prolonged time periods. Herbivores have been shown to follow phenological gradients while

[1] This manuscript is co-authored by M. Hebblewhite and F. Cagnacci and intended to be submitted to Functional Ecology.

migrating between seasonal ranges (Sawyer and Kauffman 2011, Bischof et al. 2012, Peters et al. in prep [Chapter 4]). Plant digestibility and protein content are positively correlated with elevation and latitude (Van Soest 1994). Thus, seasonal migration between lower elevation winter ranges and higher elevation summer ranges allows herbivores to track changes in forage quality, phenology or availability that maximize dietary protein (Albon and Langvatn 1992, Hebblewhite et al. 2008). Animals feeding mainly on herbivorous diet, such as giant pandas (*Ailuropoda melanoleuca*), golden takin (*Budorcas taxicolor bedfordi;* Wang et al. 2010) or North American elk or red deer (*Cervus elaphus spp*.) often follow phenological gradients to optimize nutrition (Mysterud et al. 2001a, Hebblewhite et al. 2008, Bischof et al. 2012) and several studies suggest fitness benefits. For example, in a study by Nicholson et al. (1997), mule deer (*Odoceoilus hemonius*) who had increased access to high quality forage in a mountainous region also had increased reproductive success. Female red deer that used high elevation summer ranges in Norway and elk in Canada had higher body mass and pregnancy rates than females that spent summers at lower elevations (Mysterud et al. 2001a, Hebblewhite et al. 2008).

Ungulate movements can be viewed as the integration of a sequential series of complex behaviors, and animals may make choices at very small scales of minutes to daily movements that in turn, aggregate to monthly and seasonal trajectories (Senft et al. 1987, Owen-Smith et al. 2010). Thus, under this hierarchical foraging framework herbivores display different foraging behavior at the plant, patch, landscape or regional level, trading-off forage biomass, nutritional quality and other factors to varying degrees at each scale (Senft et al. 1989). Because plants are constantly

changing in terms of biomass or forage quality, understanding the factors that explain smaller-scale movements may provide key information for the drivers of larger-scale seasonal movements (Albon and Langvatn 1992, Hopcraft et al. 2014). Several studies addressing migration in response to phenological gradients have been conducted (Sawyer and Kauffman 2011, Bischof et al. 2012, Lendrum et al. 2014), but researchers often use large-scale indexes of forage quality such as satellite derived indices (Normalized Difference Vegetation Index, NDVI; Pettorelli et al. 2005). Furthermore, most of the research on ungulate migration has focused on grazers or mixed feeders (Wilmshurst et al. 1999, Hebblewhite et al. 2008), and forage selection driving migration may be different for browsers (Owensmith and Novellie 1982, Fryxell 1991, van Beest et al. 2010).

Along the browser-grazer continuum (Hofmann 1973) roe deer (*Capreolus capreolus*) are classified as browsing concentrate selectors, relying on high-quality low fiber food items. Browsers differ from grazers (bulk roughage feeders; Hofman 1973) due to their preferences for dicots as opposed to monocots (grazers). Small browsers especially rely on ingesting relatively low amounts of high quality food to meet energy requirements (Hofmann 1989). Roe deer are considered "obligatory non-grazers", because they avoid grasses to a higher degree than grazers avoid browse (Clauss et al. 2003, Redjadj et al. 2014). These small ungulates are particularly selective for plant quality across diverse forage species (Tixier and Duncan 1996, Linnell et al. 1998). Research confirmed that biomass is not an important driver for roe deer forage selection, but rather quality (Storms et al. 2006, Barancekova et al. 2010). Lastly, roe deer are very plastic in their seasonal movement behavior. For

example, roe deer are partially migratory where only some individuals within a population migrate in any given year (Cagnacci et al. 2011; Peters et al. in prep [Chapter 3], Peters et al. in prep [Chapter 4]). Consequently, testing how spatial and temporal variation of roe deer forage and therefore nutrition, relates to different migratory strategies can provide insights into migratory plasticity (Hebblewhite et al. 2008). Despite the potential nutritional benefits of migration for browsers, few previous studies have specifically tested the bottom-up benefits of migration for browsing ruminants, in part because of the challenge of measuring forage quality.

Plant forage quality, defined as the digestibility of forage due to nutrient and fiber levels, varies between plant species, phenological stage, and even individual plant parts (Steuer et al. 2014). Besides protein content of fiber, several plant secondary compounds also affect the quality of ungulate forage (Barboza et al. 2009) and tannins are probably the most important group amongst them (Van Soest 1994). Tannins are phenolic compounds that are used by plants as anti-herbivory defense mechanisms, and are particularity high in browse forage species (Robbins 1983, Van Soest 1994). Tannins form insoluble complexes with highly-digestible proteins (e.g., nitrogen), inhibiting digestion and decreasing the nutritive value of defended plants (Van Soest 1994). Notwithstanding tannins, measuring plant forage quality availability to ruminants is challenging, because of the diversity of individual plant species often available to individual herbivores, especially in mountainous ecosystems. Instead of direct field measurements of forage quality, fecal indices are commonly used to reflect dietary forage quality in herbivores. Total fecal nitrogen (TFN) is one of the most widely used indices to quantify forage quality and organic

matter digestibility of consumed plant forage in herbivores (Leslie et al. 2008, Wang et al. 2009, Steuer et al. 2014). However, TFN has been criticized as indicator for diet quality for browsers because of the protein-binding characteristics of tannins, which biases TFN value high (Robbins 1983, Hobbs 1987). At least part of the nitrogen-binding effect of tannins can be eliminated by using related indices, such as the metabolic fecal N (MFN; Van Soest 1994). Total fecal nitrogen is mainly composed MFN, which includes microbial cells and their residues, and undigested fecal fiber-bound N (neutral-detergent insoluble, NDIN; Steuer et al. 2014). The growth of microbes in the gut of ruminants is mainly triggered by their energy supply that is tightly linked to the digestibility of the ingested diet (Lukas et al. 2005). Unlike NDIN, and consequently TFN, MFN is much less affected by tannins in the ingested diet (Van Soest 1994). Consequently, the use of MFN provides a less biased estimator of organic matter digestibility from feces of animals feeding on browse, such as roe deer, yet few studies have used MFN to investigate nutritional benefits of different foraging strategies in browsers (Steuer et al. 2014).

To understand the relationships between seasonal movements and seasonal foraging behavior in a partially migratory population of roe deer, a small browser, we asked a set of specific questions from broad to finer diet scales following Senft's foraging hierarchies (Senft et al. 1987). First, we tested whether migrant and resident individuals differed in their use of different vegetation communities during the growing season, characterized by plant cover, overstory vegetation, and plant phenology. We tested whether plant cover or overstory vegetation best separated resident and migrant roe deer throughout the growing season. Next, we tested how

phenological gradients relate to migration by roe deer. According to the green-wave-hypothesis (Owen 1980), we predicted that roe deer migrants would follow plant green-up to take advantage of ephermeral forage (Sawyer and Kaufmann 2011). Further, we predicted that roe deer undergoing altitudinal migration will have access to younger phenological stages for extended periods in contrast to resident animals due to delayed phenology at higher elevations (Hebblewhite et al. 2008). Next, we tested the prediction that migratory roe deer feed on higher quality diet than residents (Hebblewhite et al. 2008). Hence, we expected fecal nitrogen (FN) levels from migratory roe deer to be higher than FN from residents. Because roe deer are browsers, we also tested for relationships between TFN and MFN and predicted that MFN would show fewer differences in diet quality because it is less affected by tannins. Finally, one of the most energy demanding processes in ungulates is lactation and gestation, during which females require about 2-3 times the average diet intake (Barboza et al. 2009). Therefore, we predicted fecal nitrogen levels to be higher for female than for male roe deer irrespective of migratory status.

METHODS

Study Area and Animal Location Data

Our study area was a ~ 40 000 ha mountainous area in the northeastern Autonomous Province of Trento, Italy (Fig.2-1). The study area is characterized by rugged terrain with elevations ranging from 400m in the main valley bottoms to 3 500 m at the highest peaks. The climate is continental in the alpine river valleys to strongly alpine above treeline, with average annual precipitation of 1 100 mm (Ossi et al. 2015). The study area is covered to about 40% by coniferous and deciduous forests. Along the

valley bottoms agricultural grasslands and crops as well as deciduous forests, mainly comprised by European beech (*Fagus sylvatica*) and European ash (*Fraxinus excelsior*), predominate. Understory vegetation is patchily distributed and is dominated by common hazel (*Corylus avellana*) and brambles (*Rubus spp.*). Higher elevations and the narrow lateral valleys are covered by coniferous forest, mainly comprised of Norway spruce (*Picea abies*), silver fir (*Abies alba*) and European larch (*Larix decidua*). Mountain pine (*Pinus mugo*) as well as shrublands of rhododendron (*Rhododendron spp.*) interspersed with alpine grasslands prevail above elevation of 1 600 m. The fauna is amongst the richest in the Alps. Ungulate species inhabiting the region include (in order of abundance): chamois (*Rupricapra rupricapra*), roe deer, red deer, and ibex (*Capra ibex*). The predator community is characterized by foxes (*Vulpes vulpes*) and reintroduced brown bears (*Ursus actos*) at low densities. The human population density of approx. 31/km^2 is low in comparison to other parts of Italy. During winter, snow cover is normally shallow (< 20 cm) and discontinuous at the lowest elevations, but may increase to >1 m at elevations above 1 600 – 1 700 m, where it may last from December to late April (Ramanzin et al. 2007).

We used animal location data from 22 roe deer, which were captured in winters of 2012/2013 and 2013/2014 using box traps with an automatic closing mechanism at bait sites (Peterson et al. 2003). All animal capture and handling procedures were approved under University of Montana animal care regulations (AUP 060-12MHWB-113012) and the Trento Province (Wildlife Committee of the Autonomous Province of Trento, September 11th 2011). We deployed GPS-GSM radio collars (VECTRONIC Aerospace GmbH, GPS plus 3D) that were programmed

to collect animal location data every three hours. Average fix success was 0.92 (SD=0.07; Appendix A1). GPS collars were equipped with a very high-frequency (VHF) beacon and a drop-off mechanism.

Field Sampling and Sample Processing

To test for differences in overstory vegetation communities and plant phenology between roe deer with different seasonal movement strategies, we collected information on plant cover, plant phenology and fecal samples along animal movement trajectories during two growing seasons between mid-April and early October in 2013 and 2014 (Appendix 2-B). This study period is ecologically important for roe deer, because it corresponds to their reproductive season, including the establishment and defense of male territories, natal dispersal, births and the rutting period (Linnell et al. 1998). The season also includes departure and return of partially migratory roe deer. Due to incomplete GSM cellular coverage throughout the study area, we had to employ two different methods to determine sampling locations. First, for animals for which GSM coverage was available, we projected a 50m grid over the movement trajectory of animals of the previous 8 days using open-source Quantum GIS (ver. 1.8.0) software (QGIS Development Team 2014). We selected the grid cell with the highest number of animal locations and within this cell we determined the most recent GPS location as sampling location. Second, for animals for which GSM coverage was unavailable, we determined sampling locations with VHF-triangulation. We recorded ≥ 3 bearings within approximately 30 min to avoid movements by the animal (Millspaugh et al. 2012). To account for VHF triangulation error, we validated

roe deer use at estimated locations by searching for recent signs of roe deer presence, such as fresh tracks, feces and bed sites, or visual confirmation of the animal on site.

We collected data on plant communities including main vegetation type, which we defined as either the two most dominant overstory vegetation species (trees or shrubs) or meadows (including pastures, grasslands and gardens) within approximately 50 m surrounding the sampling location determined as outlined above. At the foraging-patch scale we recorded percentage ground cover by phenological stages of graminoids, forbs and shrubs within two adjacent 1m quadrats. Plant phenology was estimated as old growth, newly emergent, fruiting, flowering, mature growth and cured vegetation following Hebblewhite et al. (2008). To estimate fecal nitrogen, we collected a minimum of six fresh fecal pellets from up to three pellet heaps at used sites. Because we followed trajectories of known animals close to real-time, we were able to ensure that samples were very fresh and suitable for FN analyses. If feces are exposed to insects or weather for longer than two-three weeks, retention of nitrogen may be increased (Jenks et al. 1990). We froze fecal samples immediately at -20 C until we oven-dried them for 48 hours at 50 C to constant weight in a ventilated drying chamber. We collected a total of 673 fecal samples from the 22 individual roe deer throughout two vegetation periods.

For FN analysis, we pooled all samples collected from individual roe deer in each 16-day period (see Appendix 2-A for details on sampling and analysis intervals). Dried composite samples were ground through a 1-mm sieve and analyzed for nitrogen content using the Dumas method with a Carbon/Nitrogen gas analyzer (LECO Corporation, St Joseph, Michigan, USA). We also estimated the undigested nitrogen from the diet for about 40% of all samples based on the NDIN. Samples were boiled with neutral-

detergent solution (Van Soest, Robertson & Lewis 1991) with the Gerhardt fibre-bag system (Gerhardt, Koenigswinter, Germany). The NDF rise eliminates the metabolic nitrogen from fecal samples, which is affected mainly by microbial digestion of forages, and to a lesser degree by nitrogen recycle in saliva and cells from the digestive system of animals (Barboza et al. 2009). Then, we also estimated nitrogen of the fecal NDF residue using the Dumas method and calculated MFN as the difference between TFN and NDIN (Mason and Frederiksen 1978). Analyses of fecal samples were conducted at the Research Centre for Agriculture and Forestry, Laimburg (BZ), Italy. Our final FN samples sizes for statistical analyses were 302 TFN samples and 118 MFN samples.

Statistical Analyses

Classification of Animal Movement

We first separated individuals into either migrants or residents using previously developed methods to test the green wave hypothesis for migratory strategies in roe deer. We used GPS locations from 22 GPS-collared roe deer between February 15th of the first year and February 14th of the following year to classify migratory strategies. Some animals were sampled for two years (Table 2-1) and we considered the animal year as our sampling unit and included 36 roe deer sampling years in our statistical analyses. We employed a combination of methods, including the net-squared displacement (NSD; Bunnefeld et al. 2011), a supervised spatial clustering method (Cagnacci et al. 2011, Cagnacci et al. *in revision*) and addition visual inspection of seasonal movement trajectories to classify migration, because previous studies have clearly demonstrated that no single method performs best in classification (Cagnacci et al. *in revision*, Peters et al. in prep [Chapter 3]). The clustering analysis was conducted in SAS (SAS 2010), all other

statistical analyses were conducted in R, version 3.2.0 (R Development Core Team 2013). By our definition, migrants were also required to have non-overlapping seasonal ranges for a minimum of one month (residence time >30 days; Cagnacci et al. 2011). For roe deer that were monitored using VHF telemetry due to malfunctioning GPS collars for either the entire or part of the study period we assessed the overlap between winter (Jan, Feb, March) and summer (June, July, August) home ranges (Fryxell and Sinclair 1988). We estimated seasonal home ranges using 95% kernel density utilization distributions with a reference smoothing factor (href; Worton 1989) in adehabitat (Calenge 2006). We defined roe deer as migrants if their seasonal ranges were non-overlapping (Fryxell and Sinclair 1988). Using a combination of the described methods we identified 11 roe deer years as migratory and 25 as resident (Appendix A-1).

Seasonal Differences in Vegetation Structure

To test for differences in general vegetation structure between resident and migratory roe deer we performed a between-class analysis (herein BCA) in R library ade4 (Chessel et al. 2004) based on the phenology and cover data collected at sampling locations. First we used a multivariate Hill-Smith Analysis that allowed us to incorporate continuous and categorical variables. We partitioned the total variance into the different groups as combined factors of migration status (resident or migrant) and three time periods (early summer, ca. late April to mid-June; summer, ca. mid-June – mid-August, and late summer, ca. mid-August – late September; Appendix 2-B): thus, we compared six classes. The BCA is carried out by ordination of predefined groups and then projecting the individual sampled locations onto the resulting axes. This allowed us to identify the phenological classes and cover types that maximize the difference between

different periods and migration status. We used permutation tests with 999 permutations to assess the statistical significance of the BCA.

Plant Phenology and Fecal Nitrogen

We estimated plant phenology scores (Post and Klein 1999) by weighting the average percent cover and phenology class for each plant group, forbs, graminoids, and shrubs, to the plot level. Specifically, we followed an approach similar to Hebblewhite et al. (2008) and assigned a score representing the growth stage from 0-5, where 0=old, 1= new or emergent growth, 2=flowering, 3= fruiting, 4 = mature, and 5= cured. A phenology score weighted by percent cover then was calculated for each vegetation class and the total of all vegetation by plot.

We analyzed frequency weighted phenology scores of forbs, graminoids, shrubs, the plot total, as well as TFN and MFN (response variables) using linear models with migrant status, sampling time, year and sex as predictor variables. We considered the interactions between migrant status and year, migrant status and sampling interval and migrant status and sex. We verified that the relationships between phenological scores, TFN and MFN, and each predictor variable were linear using the loess smoothing function in R (R Development Core Team 2013). We also tested for the significance of animal identity as random factor to account for repeated measures of the same individual and unbalanced sample sizes using linear mixed models (LMM) using the R library lme4 (Bates et al. 2015). We first performed model selection on models with all possible combinations of covariates included in the full model for each dataset based on the Akaike Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002). We retained only the models within two AICc from the top model and

report coefficients and standard errors from model averaging (Arnold 2010) using the multi-model inference (MuMIN) library in R (Bartoń 2009). Because the presence of interactions in candidate models is known to artificially inflate their sums of weights, we interpreted our model averaging results cautiously if interactions are present (Galipaud et al. 2014). Because the use of TFN to assess forage quality in browsers has been much debated (Verheyden et al. 2011, Robbins 1983), we tested for significant relationships between TFN and MFN to understand if TFN can be used as an index for diet quality in roe deer. If a single variable best described the relationship between our response and predictor variables, we report model coefficients, AICc, the number of parameters and the log-likelihood in text.

RESULTS

Seasonal Differences in Vegetation Structure

We tested for differences in overstory vegetation composition, vegetation cover and phenology scores in three periods during the growing season between resident and migrant roe deer. We found statistically significant differences between these groups (Fig. 2-2, Table 2-1; BCA-test, P=0.001). The main plant species that separated roe deer habitats in early summer compared to summer and late summer (Axis 1) were *Juniperus spp*. and *Salix spp*. that were both associated with early summer ranges of residents and migrants. The second axis revealed that during summer and late summer resident and migrant roe were mostly separated by *Sorbus aucuparia* and *Laburnum alpinum* in the overstory that were more associated with resident roe deer. *Betula spp*. and *Alnus. spp*. were mainly associated with migrant roe deer (Fig. 2-2, Table 2-1). In general, vegetative habitat characteristics of residents and migrants were most similar in early summer based

on the location of class centers (Fig. 2-2). The first axis explained 61% and the second axis 17% of the total inertia.

Plant Phenology

Plant phenology scores increased throughout the vegetation period for all three forage classes, forb, graminoids, and shrubs as well as the total of all three classes (Fig. 2-3). However, we found no statistically significant differences between phenology scores and migratory status, including none of the interactions we tested. Migration status was included in top models that entered the model averaging process for graminoids and overall plant phenology, but importance weights were below 1, and coefficients only marginally significant. We report models within 2 AICc ($\Delta AIC_c \leq 2$) and the averaged coefficients in Tables 2-2 through 2-9. Significant parameters (alpha ≤ 0.1) in the top model describing forb phenology included only interval (time; β=0.051, SE=0.015, $p<0.001$; β_0 = 1.415, SE=0.123, $p<0.001$), indicating that forb phenology was only driven by time. The forb model was also the only model for which the inclusion of animal ID yielded a lower AICc (AICc= 1806.0, K=3, loglik=-898.95) compared to the top fixed effects model (AICc= 1813.9, K=2, loglik=-903.95), suggesting between-individual differences in exposure to forb phenology. The difference in AICc between the random and the fixed effects forb model was ΔAICc=7.9. Regardless, the top fixed effects model also had sampling interval as its only explanatory variable for forb phenology. Graminoid phenology throughout the vegetative season was best explained by a model averaged of five models within 2 AICc (Table 2-2). Significant parameters for graminoid phenology were sampling interval (β=0.058, SE=0.006, $p<0.001$) and sampling year, with lower phenological scores (β=-0.123, SE=0.044, $p<0.001$; i.e., delayed growing season in 2014

(Table 2-3). Shrub phenology in our study area was best described by a single model containing again only sampling interval (β=0.076, SE=0.007, p<0.001) and year (reference=2013; β=0.134, SE=0.045, p=0.003) as explanatory variables (β_0 = 0.495, SE=0.052, p<0.001, K=3, loglik=-439.49). Lastly, based on four averaged models (Table 2-4), the overall phenology at sampling plots was a function of sampling interval (β=0.063, SE=0.009, p<0.001) as the only significant predictor (Table 2-5). Thus there were no strong differences in phenology between migrant and resident roe deer in any year.

Fecal Nitrogen

When comparing migrants and residents, migrants had higher TFN and MFN than residents in both years (Fig. 2-4). TFN was best predicted by three models within two AICc (Table 2-6), which we model averaged (Table 2-7). The averaged final model included the interaction (β=0.097, SE=0.030, p=0.001) between migration status and sampling interval and their main effects, as well as year, and sex. However, only the migrant-time interaction and their main effects had an importance weight of 1 (Table 2-7). Overall, TFN decreased throughout the sampling period, but more rapidly for resident roe deer than migrant roe deer (Fig. 2-5). The best model predicting MFN was averaged based on five models within 2 AICc (Table 2-8) and contained and sex in addition to two interactions; migration and sampling interval as well as migration and year and their main effects (Table 2-9). Significant coefficients were the sampling interval (β=-0.077, SE=0.022, p<0.001), migration status (β=0.310, SE=0.256, p=0.043) and year (β=0.395, SE=0.190, p<0.001) terms. The interaction between migration and sampling interval was only marginally significant (β=0.057, SE=0.034, p=0.099). Overall the averaged model

showed MFN decreased more strongly for migrants than for residents (Fig. 2-5). On average MFN was higher in 2014 compared to 2013.

Lastly, we found that TFN and MFN were strongly correlated (Fig. 2-6) with a Pearson's correlation coefficient of r= 0.81 (t= 14.90, df =115, p<0.001). The linear relationship between TFN and MFN had an intercept of β_0 = 1.88 (SE=0.11, p<0.001) and the coefficient for MFN was β_{MFN} = 0.87 (SE = 0.06, p<0.001). This indicates that while tannins seem to reduce diet quality for roe deer (both the slope <1 and the positive Y intercept), the magnitude of the effect was small, and TFN and MFN were very highly correlated for roe deer.

DISCUSSION

Our results suggest that migratory roe deer ingested forage of higher quality than resident roe deer, consistent with the green-wave hypothesis, but, counterintuitively, broad plant phenology did not differ between both groups. Instead of delayed plant phenology driving higher forage quality in migrant roe deer, broad vegetation composition differences may explain the higher dietary forage quality of migrants as the mechanism. We found migrant and resident roe deer occurred in habitats of similar vegetation structure in early summer, but then their habitats diverged increasingly towards late summer, when FN also diverged the most regardless of which measure (TFN or MFN) we used. This suggests that while phenological development was similar between resident and migrant ranges, the vegetation communities in which they occurred varied, potentially offering different foraging plants of different diet quality. Our results confirm that roe deer foraging behavior results in nutritionally higher quality for migrants, consistent with the green-wave hypothesis, but for different mechanisms than phenology.

Alternatively, a missing piece of this puzzle could be finer scale diet selection by migrant roe deer for specific species or higher quality plant parts at the bite scale (Senft et al. 1987). Nevertheless, our results show that roe deer foraging behavior is diverse and needs to be evaluated considering combined effects of ecological and behavioral mechanisms (Senft et al. 1987, Redjadj et al. 2014).

At larger scales of general vegetation community characteristics, summer and late summer ranges of migratory roe deer were stronger associated with *Alnus spp*, *Abies spp*. and *Betula spp.*, which suggest use of montane and sub-montane forest, but also riparian zones (Pignatti and Pignatti 2000). In contrast, resident summer ranges were more associated with *Sorbus aucuparia* (rowan) and *Laburnum alpinum*, which are both common at lower elevations in the Dolomites and often occur in younger, regenerating forests in association with *Fraxinus excelsior*. In the same study area, roe deer in general (no differentiation between migrants and residents) selected for higher canopy cover and younger forest stands with more forage species over climax environments (Mancinelli et al. *in revision*). The same study showed that roe deer are selective at small spatial and temporal scales within their seasonal ranges. These results point towards the hierarchical nature of ungulate foraging behavior (Senft et al. 1987). For example Hebblewhite et al. (2008) showed that migratory elk had consistently higher forage quality than their resident counterparts, which in that case was a result of different phenological availability between strategies that was itself driven by large-scale habitat selection.

In contrast to this example for elk, we found no statistically significant differences in plant phenology, but FN levels differed between resident and migrant roe deer. Especially, due to the high spatiotemporal diversity in biomass and plant quality,

ungulates in alpine environments can be selective for forage at different spatial scales (Hebblewhite et al. 2008, Zweifel-Schielly et al. 2012). Rugged alpine landscapes commonly offer increased fine-scale spatiotemporal variability in foraging conditions (Albon and Langvatn 1992, Zweifel-Schielly et al. 2012). This is also reflected by the fact that our frequency weighed phenology scores never reached the maximum value of five for both migrants and residents, which would indicate senescence of all plants within a vegetation category. Notably, our study area is also very moist, more so than western North American landscapes for example where more pronounced phenological differences have been the main driver of higher FN of migratory ungulates (Hebblewhite et al. 2008). High rainfall through to the end of the growing season may minimize the phenological differences between resident and migrant ranges in this moist system. Both topographic variation and high precipitation thus likely maintain high phenological diversity throughout the vegetative season equally for residents and migrants. Alternatively, resident roe deer could have been more selective at finer-scales than we could measure during our phenology plot-based sampling (Senft et al. 1987, Johnson et al. 2001). As a pure browser (Hofmann 1973, Van Soest 1994) roe deer can forage on a wide range of high quality plants with a strong seasonal diet specialization (Duncan et al. 1998, Cornelis et al. 1999). Consequently, there may have been discrepancies between the locations that we sampled for plant phenology and feces, and the site where the animal foraged although roe deer have rather short retention times of less than 24 hrs (Behrend et al. 2004). Also, we may have been unable to estimate the phenological diversity of our alpine study area as well as the fine-scale micro-site selectivity of roe deer with our vegetation sampling design. Interestingly, also Zini (2015) found no

differences in shrub phenology and abundance between migrants and residents during summer in the same study area. Despite these potential problems, the results from FN analysis confirm that migratory roe deer made different foraging decisions at finer-scales than the one we sampled for plant phenology.

Our results that migratory roe deer seem to have access to higher forage based on FN are the first in the literature to suggest that the green-wave hypothesis might also apply to browsing ungulates and match findings from other studies on mixed feeders or grazers, despite the mechanism not being phenologically driven. For example, Hebblewhite et al. (2008) found that migratory elk had higher diet quality measured by FN and forage digestibility compared to resident individuals in a partially migratory population. In this study, Hebblewhite et al. (2008) showed that differences were consistent with broad scale habitat selection that resulted in different phenological availability between migrants and residents, as well as finer-scale diet differences between strategies. Gaidet and Lecomte (2013) found that diet quality and body condition was higher in migratory compared to resident impalas (*Aepyceros melampus*) in Zimbabwe, and hypothesized the difference was also driven by habitat availability, not phenology. For migratory mule deer (*Odocoileus hemionus*) in California, FN corresponded well to changes in the Normalized Difference Vegetation Index (NDVI) and both indices suggested nutritional benefits of migration (Lendrum et al. 2014). Lastly, Sakuragi et al. (2002) suggested that in a partially migratory sika deer (*Cervus nippon*) population in Japan only altitudinal migrants had a nutritional advantage based on FN, and this was thought to be driven by both phenological and diet differences. In our study, roe deer were largely altitudinal migrants (Appendix 2-

C), which surprisingly did not change phenology, but resulted in significant differences in the availability of plant communities especially during late summer and autumn when differences in FN were the greatest between migrants and residents.

Our results also revealed that the high level of tannins in browse species may not pose a major limitation to roe deer forage quality. Browse species are rich in tannins and lignin, preventing nutrients to be easily digested (Barboza et al. 2009), but roe deer have developed several mechanisms to cope with tannins, including tannin-binding agents in their saliva that may inactivate free tannins in forage (Fickel et al. 1998) and their disproportionately large livers that have been found to deactivate plant toxins (Cheeke 1994). Here, we found that TFN and MFN were highly correlated for roe deer, with only a modest difference from being equivalent (13% lower MFN than TFN). Unlike other studies that were able to measure the loss of digestible nitrogen from captive trials (Hanley et al. 1992), TFN is the sum of MFN and fiber bound N including tannins. Thus, we were unable to estimate the loss of digestive efficiency because of tannins with MFN. Regardless, the strong linear relationship between the two that we report suggests that, at least for roe deer in our study area, TFN is a reliable indicator of diet quality. In contrast, Verheyden et al. (2011) suggested that there were strong non-linearities between TFN and dietary nitrogen in a study based on feeding trials of captive roe deer depending on the tannin content of forage. These authors indicate that dietary nitrogen increases with TFN when the dietary condensed tannin is low or absent, but the relationship disappears when there is an appreciable amount of condensed tannin in the diet (2%). Consequently, our results suggest that roe deer in our study areas seem to ingest rather low amounts of tannin rich diet

throughout the summer. High spatiotemporal diversity and favorable weather conditions may allow such high selectivity by roe deer in our study area.

The relationship between dietary nitrogen and FN are affected by complex factors and tannin levels in plants change dramatically through the growing season (Hanley et al. 1992). High temperatures, water stress, extreme light intensities, poor soil quality as well as differences in herbivory increase the tannin content of plants (Van Soest 1994). There is also substantial seasonal variation in tannin content related to periods of somatic growth, flowering, and seeding. Overall, relationships between season and tannin content are difficult to generalize and likely to change between plant and animal species due to the large diversity of tannins and the specificity of defenses in consumers (Makkar 2003). Nonetheless, our results show that roe deer may only lose modest amounts of available energy due to tannins, supporting the use of TFN and MFN in browsers such as roe deer to gauge dietary forage quality.

Interestingly, we found no differences in plant phenology or diet quality between sexes. However, sex was included as predictor variable in top models with two ΔAICc and coefficients suggest slightly lower values of TFN and MFN in male roe deer. Yet, these differences were not statistically significant potentially also due to our low sample sizes (12 male sampling years compared to 24 female sampling years). Further though it is possible that roe deer in general show smaller dietary difference between sexes due to a variety of reasons. For example, this small cervid shows almost no sexual size dimorphism (Andersen et al. 2000). Also, roe deer are considered income breeders and therefore the late spring and summer seasons are critical for their fitness (Andersen et al. 2000). While, energy requirements are

elevated during summer for females (end of gestation, lactation) also males require forage of high nutritional value due to territoriality and rutting behavior (Hewison et al. 1998). Thus, both sexes may select forage that is that is highly digestible and rich in soluble carbohydrates (Duncan et al. 1998). Mysterud et al. (1999) found no differences in food selection between sexes in winter.

In conclusion, the foraging process is generally very complex in large herbivores and must be interpreted by considering behavioral mechanisms ranging from space use at larger scales to the fine-scale selection of plant parts at the bite-scale (Redjadj et al. 2014). We found evidence that roe deer benefit from migration, but not because of the phenological mechanisms of the green-wave hypothesis, as we found no evidence for differences in phenology in our system. Instead, roe deer consume a high diversity of plant species that are strongly dependent on the plant species availability within different habitats (Tixier and Duncan 1996, Cornelis et al. 1999). Our between class analysis suggested that general vegetation communities, and thus, forage species availability differed between migration strategies. Thus, broad-scale habitat selection, especially during late summer and autumn, may set the availability stage for higher quality forage for migrants, not phenology per se. Forage selection at a finer scale than we studied here (e.g., plant species, parts) may also contribute to higher forage quality in migrant roe deer. However, assessing diet for roe deer is challenging as they typically ingest very diverse forage in a single study area (Verheyden et al. 2011). Therefore, new methods offering the identification of specific plant items eaten may provide important insights into how large scale forage selection relates to FN values. Among such methods DNA-barcoding (Raye et al.

2011) as well as video technology deployed on radio-collars have been shown to offer increased accuracy compared traditional microhistology methods (Newmaster et al. 2013).

LITERATURE CITED

Albon, S. D. and R. Langvatn. 1992. Plant Phenology and the Benefits of Migration in a Temperate Ungulate. Oikos 65:502-513.

Andersen, R., J. M. Gaillard, J. D. C. Linnell, and P. Duncan. 2000. Factors affecting maternal care in an income breeder, the European roe deer. Journal of Animal Ecology 69:672-682.

Arnold, T. W. 2010. Uninformative Parameters and Model Selection Using Akaike's Information Criterion. Journal of Wildlife Management 74:1175-1178.

Avgar, T., I. Giladi, and R. Nathan. 2008. Linking traits of foraging animals to spatial patterns of plants: social and solitary ants generate opposing patterns of surviving seeds. Ecology Letters 11:224-234.

Barancekova, M., J. Krojerova-Prokesova, P. Sustr, and M. Heurich. 2010. Annual changes in roe deer (*Capreolus capreolus* L.) diet in the Bohemian Forest, Czech Republic/Germany. European Journal of Wildlife Research 56:327-333.

Barboza, P. S., K. L. Parker, and I. D. Hume. 2009. Integrative Wildlife Nutrition. Springer-Verlag Heidelberg, Germany.

Bartoń, K. 2009. MuMIn: multi-model inference.

Bates, D. W., B. M. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models using lme4. Journal of Statistical Software.

Behrend, A., M. Lechner-Doll, W. J. Streich, and M. Clauss. 2004. Seasonal faecal excretion, gut fill, liquid and particle marker retention in mouflonOvis ammon musimon, and a comparison with roe deerCapreolus capreolus. Acta Theriologica 49:503-515.

Bischof, R., L. E. Loe, E. L. Meisingset, B. Zimmermann, B. Van Moorter, and A. Mysterud. 2012. A Migratory Northern Ungulate in the Pursuit of Spring: Jumping or Surfing the Green Wave? American Naturalist 180:407-424.

Bunnefeld, N., L. Boerger, B. van Moorter, C. M. Rolandsen, H. Dettki, E. J. Solberg, and G. Ericsson. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. Journal of Animal Ecology 80:466-476.

Burnham, K. P. and R. A. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, USA.

Cagnacci, F., S. Focardi, A. Ghisla, B. Van Moorter, E. Gurarie, M. Heurich, A. Mysterud, J. Linnell, M. Panzacchi, and M. Roel. in revision. How many routes lead to migration? Re-establishing the link between definitions, methods and movemet ecology. Journal of Animal Ecology.

Cagnacci, F., S. Focardi, M. Heurich, A. Stache, A. J. M. Hewison, N. Morellet, P. Kjellander, J. D. C. Linnell, A. Mysterud, M. Neteler, L. Delucchi, F. Ossi, and F.

Urbano. 2011. Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. Oikos 120:1790-1802.
Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197: 516-519
Cheeke, P. R. 1994. A Review of the Functional and Evolutionary Roles of the Liver in the Detoxification of Poisonous Plants with Special Reference to Pyrrolizidine Alkaloids. Veterinary and Human Toxicology 36:240-247.
Chessel, D., A. B. Dufour, and J. Thioulouse. 2004. The ade4 package-I- One-table methods. R News. 4: 5-10.
Clauss, M., M. Lechner-Doll, and W. J. Streich. 2003. Ruminant Diversification as an Adaptation to the Physicomechanical Characteristics of Forage. A Reevaluation of an Old Debate and a New Hypothesis. Oikos 102:253-262.
Cornelis, J., J. Casaer, and M. Hermy. 1999. Impact of season, habitat and research techniques on diet composition of roe deer (Capreolus capreolus): a review. Journal of Zoology 248:195-207.
Duncan, P., H. Tixier, R. R. Hofman, and M. Lechner-Doll. 1998. Feeding strategies and the physiology of digestion in roe deer. Pages 91-116 *in* R. Andersen, P. Duncan, and J. Linnell, editors. The European roe deer: the biology of success. Scandinavian University Press, Oslo.
Eggeman, S. L., M. Hebblewhite, H. Bohm, J. Whittington, and E. H. Merrill. in revision. Behavioral Flexibility in Migratory Behavior in a Long-Lived Large Herbivore. Journal of Animal Ecology.
Fickel, J., F. Goritz, B. A. Joest, T. Hildebrandt, R. R. Hofmann, and G. Breves. 1998. Analysis of parotid and mixed saliva in Roe deer (*Capreolus capreolus* L.). Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology 168:257-264.
Fieberg, J., D. W. Kuehn, and G. D. DelGiudice. 2008. Understanding Variation in Autumn Migration of Northern White-Tailed Deer by Long-Term Study.
Fryxell, J. M. 1991. Forage Quality and Aggregation by Large Herbivores. American Naturalist 138:478-498.
Fryxell, J. M., J. Greever, and A. R. E. Sinclair. 1988. Why are ungulate so abundant. American Naturalist 131:781-798.
Fryxell, J. M. and A. R. E. Sinclair. 1988. Causes and Consequences of Migration by Large Herbivores. Trends in Ecology & Evolution 3:237-241.
Fryxell, J. M., J. F. Wilmshurst, A. R. E. Sinclair, D. T. Haydon, R. D. Holt, and P. A. Abrams. 2005. Landscape scale, heterogeneity, and the viability of Serengeti grazers. Ecology Letters 8:328-335.
Gaidet, N. and P. Lecomte. 2013. Benefits of migration in a partially-migratory tropical ungulate. BMC Ecology 13.
Galipaud, M., Gillingham, M.A.F., David, M., Dechaume-Moncharmont, F.-X., 2014. Ecologists overestimate the importance of predictor variables in model averaging: a plea for cautious interpretations. Methods in Ecology and Evolution 5, 983-991.
Hanley, T. A., C. T. Robbins, A. E. Hagerman, and C. McArthur. 1992. Predicting Digestible Protein and Digestible Dry Matter in Tannin-Containing Forages Consumed by Ruminants. Ecology 73:537-541.

Hebblewhite, M., E. Merrill, and G. McDermid. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. Ecological Monographs 78:141-166.

Hewison, A. J. M., J.-P. Vincent, and D. Reby. 1998. Social organisation of European roe deer.

Hobbs, N. T. 1987. Fecal Indexes to Dietary Quality - a Critique. Journal of Wildlife Management 51:317-320.

Hofmann, R. R. 1973. The ruminant stomach: stomach structure and feeding habits of East African game ruminants. . Pages pp. 1–364. *in* T. R. Odhiambo, editor. East African Monographs in Biology, vol. 2. East African Literature Bureau, Nairobi.

Hofmann, R. R. 1989. Evolutionary Steps of Ecophysiological Adaptation and Diversification of Ruminants - a Comparative View of Their Digestive-System. Oecologia 78:443-457.

Hopcraft, J. G. C., J. Morales, H. Beyer, M. Borner, E. Mwangomo, A. Sinclair, H. Olff, and D. T. Haydon. 2014. Competition, predation, and migration: individual choice patterns of Serengeti migrants captured by hierarchical models. Ecological Monographs 84:355-372.

Jenks, J. A., R. B. Soper, R. L. Lochmiller, and D. M. Leslie, Jr. 1990. Effect of Exposure on Nitrogen and Fiber Characteristics of White-Tailed Deer Feces. The Journal of Wildlife Management 54:389-391.

Johnson, C. J., K. L. Parker, and D. C. Heard. 2001. Foraging across a variable landscape: behavioral decisions made by woodland caribou at multiple spatial scales. Oecologia 127:590-602.

Lendrum, P. E., C. R. Anderson Jr, K. L. Monteith, J. A. Jenks, and R. T. Bowyer. 2014. Relating the movement of a rapidly migrating ungulate to spatio-temporal patterns of forage quality. Mammalian Biology - Zeitschrift für Säugetierkunde 79:369-375.

Leslie, D. M., R. T. Bowyer, and J. A. Jenks. 2008. Facts From Feces: Nitrogen Still Measures Up as a Nutritional Index for Mammalian Herbivores. Journal of Wildlife Management 72:1420-1433.

Linnell, J. D. C., P. Duncan, and R. Andersen. 1998. The European roe deer: A portrait of a successfulk species.*in* R. Andersen, P. Duncan, and J. D. C. Linnell, editors. *The European roe deer: the biology of success*. Scandinavian University Press, Oslo.

Lukas, M., K.-H. Südekum, G. Rave, K. Friedel, and A. Susenbeth. 2005. Relationship between fecal crude protein concentration and diet organic matter digestibility in cattle. Journal of Animal Science 83:1332-1344.

Makkar, H. P. S. 2003. Effects and fate of tannins in ruminant animals, adaptation to tannins, and strategies to overcome detrimental effects of feeding tannin-rich feeds. Small Ruminant Research 49:241-256.

Mason, V. C. and J. H. Frederiksen. 1978. Partition of the nitrogen in sheep faeces with detergent solutions, and its application to the estimation of the true digestibility of dietary nitrogen and the excretion of non dietary faecal nitrogen. Zeitschrift für Tierphysiologie Tierernährung und Futtermittelkunde 41:121-131.

Millspaugh, J., D. Kesler, R. Kays, R. Gitzen, J. Schulz, C. Rota, C. Bodinof, J. Belant, and B. Keller. 2012. Wildlife radiotelemetry and remote monitoring. The wildlife techniques manual 1:258-283.

Mysterud, A., R. Langvatn, N. G. Yoccoz, and N. C. Stenseth. 2001a. Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. Journal of Animal Ecology 70:915-923.

Mysterud, A., L. B. Lian, and D. O. Hjermann. 1999. Scale-dependent trade-offs in foraging by European roe deer (Capreolus capreolus) during winter. Canadian Journal of Zoology-Revue Canadienne De Zoologie 77:1486-1493.

Mysterud, A., F. J. Perez-Barberia, and I. J. Gordon. 2001b. The effect of season, sex and feeding style on home range area versus body mass scaling in temperate ruminants. Oecologia 127:30-39.

Newmaster, S. G., I. D. Thompson, R. A. D. Steeves, A. R. Rodgers, A. J. Fazekas, J. R. Maloles, R. T. McMullin, and J. M. Fryxell. 2013. Examination of two new technologies to assess the diet of woodland caribou: video recorders attached to collars and DNA barcoding. Canadian Journal of Forest Research 43:897-900.

Nicholson, M. C., R. T. Bowyer, and J. G. Kie. 1997. Habitat selection and survival of mule deer: Tradeoffs associated with migration. Journal of Mammalogy 78:483-504.

Ossi, F., J. M. Gaillard, M. Hebblewhite, and F. Cagnacci. 2015. Snow sinking depth and forest canopy drive winter resource selection more than supplemental feeding in an alpine population of roe deer. European Journal of Wildlife Research 61.

Owen-Smith, N., J. M. Fryxell, and E. H. Merrill. 2010. Foraging theory upscaled: the behavioural ecology of herbivore movement. Philosophical Transactions of the Royal Society B-Biological Sciences 365:2267-2278.

Owen, M. 1980. Wild geese of the world. Their Life and Ecology. B. T. Batsford Ltd. London.

Owensmith, N. and P. Novellie. 1982. What Should a Clever Ungulate Eat. American Naturalist 119:151-178.

Peterson, M. N., R. R. Lopez, P. A. Frank, M. J. Peterson, and N. J. Silvy. 2003. Evaluating capture methods for urban white-tailed deer. Wildlife Society Bulletin 31:1176-1187.

Pettorelli, N., F. Pelletier, A. Von Hardenberg, M. Festa-Bianchet, and S. D. Cote. 2007. Early onset of vegetation growth vs. rapid green-up: impacts on juvenile mountain ungulates. Ecology 88:381-390.

Pettorelli, N., J. O. Vik, A. Mysterud, J. M. Gaillard, C. J. Tucker, and N. C. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology & Evolution 20:503-510.

Pignatti, S. and M. Pignatti. 2000. Plant life of the dolomites.

Pompanon, F., E. Coissac, and P. Taberlet. 2011. Metabarcoding a new way to analyze biodiversity. Biofutur:30-32.

Post, E. and D. R. Klein. 1999. Caribou Calf Production and Seasonal Range Quality during a Population Decline. The Journal of Wildlife Management 63:335-345.

QGIS Development Team. 2014. QGIS Geographic Information System. . Open Source Geospatial Foundation Project.

R Development Core Team. 2013. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. .

Ramanzin, M., E. Sturaro, and D. Zanon. 2007. Seasonal migration and home range of roe deer (Capreolus capreolus) in the Italian eastern Alps. Canadian Journal of Zoology-Revue Canadienne De Zoologie 85:280-289.
Raye, G., C. Miquel, E. Coissac, C. Redjadj, A. Loison, and P. Taberlet. 2011. New insights on diet variability revealed by DNA barcoding and high-throughput pyrosequencing: chamois diet in autumn as a case study. Ecological Research 26:265-276.
Redjadj, C., G. Darmon, D. Maillard, T. Chevrier, D. Bastianelli, H. Verheyden, A. Loison, and S. Saïd. 2014. Intra- and Interspecific Differences in Diet Quality and Composition in a Large Herbivore Community. PloS one 9:e84756.
Robbins, C. T. 1983. Wildlife feeding and nutrition. Academic Press, New York, New York, USA.
SAS. 2010. SAS software 9.3 SAS Institute Inc., Cary, North Carolina, USA.
Sawyer, H. and M. J. Kauffman. 2011. Stopover ecology of a migratory ungulate. Journal of Animal Ecology 80:1078-1087.
Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. Bioscience 37:789-795 & 798-799.
Steuer, P., K.-H. Südekum, T. Tütken, D. W. H. Müller, J. Kaandorp, M. Bucher, M. Clauss, and J. Hummel. 2014. Does body mass convey a digestive advantage for large herbivores? Functional Ecology 28:1127-1134.
Storms, D., S. Said, H. Fritz, J. L. Hamann, C. Saint-Andrieux, and F. Klein. 2006. Influence of hurricane Lothar on red and roe deer winter diets in the Northern Vosges, France. Forest Ecology and Management 237:164-169.
Tixier, H. and P. Duncan. 1996. Are European roe deer browsers? A review of variations in the composition of their diets. Revue D Ecologie-La Terre Et La Vie 51:3-17.
van Beest, F. M., A. Mysterud, L. E. Loe, and J. M. Milner. 2010. Forage quantity, quality and depletion as scale-dependent mechanisms driving habitat selection of a large browsing herbivore. Journal of Animal Ecology 79:910-922.
Van Soest, P. J. 1994. Nutritional Ecology of the Ruminant. Cornell University, O & B Books Inc., NW Kline Place, USA.
Verheyden, H., L. Aubry, J. Merlet, P. Petibon, B. Chauveau-Duriot, N. Guillon, and P. Duncan. 2011. Faecal nitrogen, an index of diet quality in roe deer Capreolus capreolus? Wildlife Biology 17:166-175.
Wang, C. J., B. M. Tas, T. Glindemann, G. Rave, L. Schmidt, F. Weißbach, and A. Susenbeth. 2009. Fecal crude protein content as an estimate for the digestibility of forage in grazing sheep. Animal Feed Science and Technology 149:199-208.
Wang, T. J., A. K. Skidmore, Z. G. Zeng, P. S. A. Beck, Y. L. Si, Y. L. Song, X. H. Liu, and H. H. T. Prins. 2010. Migration Patterns of Two Endangered Sympatric Species from a Remote Sensing Perspective. Photogrammetric Engineering and Remote Sensing 76:1343-1352.
Wilmshurst, J. F., J. M. Fryxell, B. P. Farm, A. R. E. Sinclair, and C. P. Henschel. 1999. Spatial distribution of Serengeti wildebeest in relation to resources. Canadian Journal of Zoology-Revue Canadienne De Zoologie 77:1223-1232.
Worton, B. J. 1989. Kernel Methods for estimating the utilization distribution in home-range studies. Ecology 70:194-168.

Zini, V. 2015. Tattiche di movimento contrastanti e differenze nell'utilizzo dell'habitat del capriolo (Capreolus capreolus) a livello stagionale in ambiente alpino. Univerity of Rome - La Sapienza, Rome.

Zweifel-Schielly, B., Y. Leuenberger, M. Kreuzer, and W. Suter. 2012. A herbivore's food landscape: seasonal dynamics and nutritional implications of diet selection by a red deer population in contrasting Alpine habitats. Journal of Zoology 286:68-80.

Table 2-1. Column normed scores and class normed scores of the two axes from a Hill-Smith (HS)-between class analysis (BCA) describing differences in vegetation communities used by resident (N=25) and migrant (N=11) roe deer (*Capreolus capreolus*) based on vegetation community characteristics including vegetation cover (%) and phenology classes (measured in 2 x $1m^2$ quadrats) by plant groups (continuous variables) and overstory habitat types (characterizing the area around quadrats, ca. 50m radius; factor). Vegetation data were collected in three periods (early summer, ca. late April to mid-June; summer, ca. mid-June – mid-August, and late summer, ca. mid-August – late September) along movement trajectories of roe deer in two years (N_{2013}=14, N_{2014}=22). For detailed information on sampling intervals see Appendix 2-B.

	Axis 1	**Axis 2**
Column normed scores		
Forb Cover	0.23	-0.43
Grass Cover	0.20	0.32
Shrub Cover	0.27	0.01
Forb Phenology	0.41	0.04
Grass Phenology	0.14	0.26
Shrub Phenology	0.40	0.17
Abies alba	0.61	-2.06
Acer spp.	0.06	-0.26
Alnus spp.	0.45	-2.40
Betula spp.	-0.35	-2.23

Table 2-1 continued

Larix decidua	0.79	-1.37
Corylus avellana	-0.19	0.00
Fagus sylvatica	-0.05	0.27
Meadow	0.08	0.60
Fraxinus spp.	0.35	0.91
Juniperus spp.	-1.45	-0.14
Laburnum alpinum	-0.15	1.76
Carpinus betulus	0.49	-1.31
Picea abies	-0.10	-0.66
Pinus mugo	0.85	-1.08
Pinus sylvestris & P. nigra	-0.21	1.31
Quercus spp.	0.50	-0.47
Salix spp.	-1.25	0.38
Sorbus aucuparia	1.15	3.66
Class normed scores		
Spring - Migrant	-1.30	-0.07
Summer - Migrant	0.67	-2.07
Autumn - Migrant	1.37	-0.63
Spring - Resident	-1.12	0.18
Summer - Resident	0.45	-0.22
Autumn - Resident	1.03	1.76

Table 2-2. List of statistical models predicting phenology of graminiods (Gramin.pheno) available to a partially migratory roe deer (*Capreolus capreolus*) population during vegetative periods in 2013 and 2014 in the Dolomites in northern Italy. Covariates were time (interval), migratory status, sex reference category = males) and sampling year (reference category = 2013). Top models were retained by model selection based on AICc ($\Delta AIC_c < 2$). We report the number of parameters (K), the log-likelihood (loglik), the Akaike Information Criterion for small sample sizes (AIC_c) and the delta AICc (ΔAIC_c).

Candidate models ($\Delta AIC_c < 2$)	**K**	**loglik**	**AICc**	**ΔAIC_c**
Gramin.pheno ~ interval + migration + year	4	-370.41	750.9	0
Gramin.pheno ~ interval + migration * year	6	-369.89	751.9	1.00
Gramin.pheno ~ interval + migration + sex+ year	5	-370.11	752.4	1.44
Gramin.pheno ~ interval + year	3	-372.24	752.6	1.62
Gramin.pheno ~ interval * migration + year	6	-370.26	752.7	1.73

Table 2-3. Model averaged coefficients (β) predicting graminoid phenology available to a partially migratory roe deer (*Capreolus capreolus*) population during vegetative periods in 2013 and 2014 in the Dolomites in northern Italy. We provide standard errors (SE), p-values and the predictor's weight of the covariates included in the five models within 2 AICc of the top model (see Table 2-2).

Covariate	Averaged β	SE	p	Pred. weight
interval	0.058	0.006	<0.001	1
sex (m)	0.034	0.044	0.439	0.16
migration (m)	0.065	0.060	0.274	0.85
migration * interval	0.007	0.012	0.580	0.2
migration * year	0.086	0.085	0.581	0.14
year (2014)	-0.123	0.044	0.005	1
intercept	0.663	0.050	<0.001	/

Table 2-4. List of statistical models plant predicting phenology (Plot.pheno) available to a partially migratory roe deer (*Capreolus capreolus*) population during vegetative periods in 2013 and 2014 in the Dolomites in northern Italy. Covariates were time (interval), migratory status, sex reference category = males) and sampling year (reference category = 2013). Top models were retained by model selection based on AICc ($\Delta AIC_c < 2$). We report the number of parameters (K), the log-likelihood (loglik), the Akaike Information Criterion for small sample sizes (AIC_c) and the delta AICc (ΔAIC_c).

Candidate models ($\Delta AIC_c < 2$)	K	loglik	AIC_c	ΔAIC_c
Plot.pheno ~ interval	2	-529.03	1064.1	0
Plot.pheno ~ interval + sex	3	-528.24	1064.6	0.46
Plot.pheno ~ migration * interval	5	-527.79	1065.7	1.59
Plot.pheno ~ migration + interval	3	-528.88	1065.8	1.73

Table 2-5. Model averaged coefficients (β) predicting overall plant phenology available to a partially migratory roe deer (*Capreolus capreolus*) population during vegetative periods in 2013 and 2014 in the Dolomites in northern Italy. We provide standard errors (SE), p-values and the predictor's weight of the covariates included in the five models within 2 AICc of the top model (see Table 2-4).

Covariate	Averaged β	SE	p	Pred. weight
interval	0.063	0.009	<0.001	1
sex (m)	0.070	0.056	0.213	0.3
migration (m)	-0.101	0.111	0.361	0.33
Migration * interval	0.024	0.016	0.143	0.17
intercept	1.102	0.060	<0.001	/

Table 2-6. List of models predicting total fecal nitrogen (TFN; N=302) in roe deer (*Capreolus capreolus*) fecal pellets retained by model selection based on AICc (ΔAICc < 2). We report the number of parameters (K), the log-likelihood (loglik), the Akaike Information Criterion for small sample sizes (AIC_c) and finally the Delta AICc (ΔAIC_c). Fecal pellets were collected over two vegetation seasons in 2013 and 2014 in the Dolomites in northern Italy.

Candidate models ($\Delta AIC_c < 2$)	K	loglik	AIC_c	ΔAIC_c
TFN ~ migration * interval + year	5	-231.79	475.9	0
TFN ~ migration * interval	4	-233.70	477.6	1.73
TFN ~ migration * interval + sex + year	6	-231.72	477.9	1.98

Table 2-7. Model averaged coefficients (β) predicting total fecal nitrogen (TFN) in roe deer (*Capreolus capreolus)* fecal pellets, their standard errors (SE), p-values and the predictor's weight of the covariates included in the three models within 2 AIC_c of the top model (see Table 2-6). Fecal pellets were collected over two vegetation seasons in 2013 and 2014 in the Dolomites in northern Italy.

Covariate	Averaged β	SE	p	Pred. weight
migration (m)	-0.274	0.196	0.164	1
interval	-0.120	0.179	<0.001	1
year (2014)	0.143	0.074	0.055	0.76
migration * interval	0.097	0.030	0.001	1
sex (m)	-0.030	0.083	0.721	0.21
intercept	3.958	0.290	<0.001	/

Table 2-8. List of models predicting metabolic fecal nitrogen (MFN; N=118) in roe deer (*Capreolus capreolus)* fecal pellets retained by model selection based on AICc (ΔAICc < 2). We report the number of parameters (K), the log-likelihood (loglik), the Akaike Information Criterion for small sample sizes (AIC_c) and finally the Delta AICc (ΔAIC_c). Fecal pellets were collected over two vegetation seasons in 2013 and 2014 in the Dolomites in northern Italy.

Candidate models ($\Delta AIC_c < 2$)	K	loglik	AIC_c	ΔAICc
MFN ~ migration * interval + year	5	-85.53	183.8	0.00
MFN ~ migration + interval + year	4	-86.94	184.4	0.60
MFN ~ migration * interval + migration * year	6	-85.03	185.1	1.26
MFN ~ migration * interval + sex + year	6	-85.11	185.2	1.43
MFN ~ migration + interval + migration * year	5	-86.49	185.7	1.92

Table 2-9. Model averaged coefficients (β) predicting metabolic fecal nitrogen (MFN) in roe deer (*Capreolus capreolus)* fecal pellets, their standard errors (SE), p-values and the predictor's weight of the covariates included in the five models within 2 AIC_c of the top model (see Table 2-8). Fecal pellets were collected over two vegetation seasons in 2013 and 2014 in the Dolomites in northern Italy.

Covariate	Averaged β	SE	p	Pred. weight
migration (m)	0.310	0.256	0.043	1
interval	-0.077	0.022	<0.001	1
year (2014)	0.395	0.109	<0.001	1
migration * interval	0.057	0.034	0.099	0.64
migration * year	-0.187	0.195	0.342	0.29
sex (m)	-0.096	0.107	0.377	0.16
intercept	1.980	0.153	<0.001	/

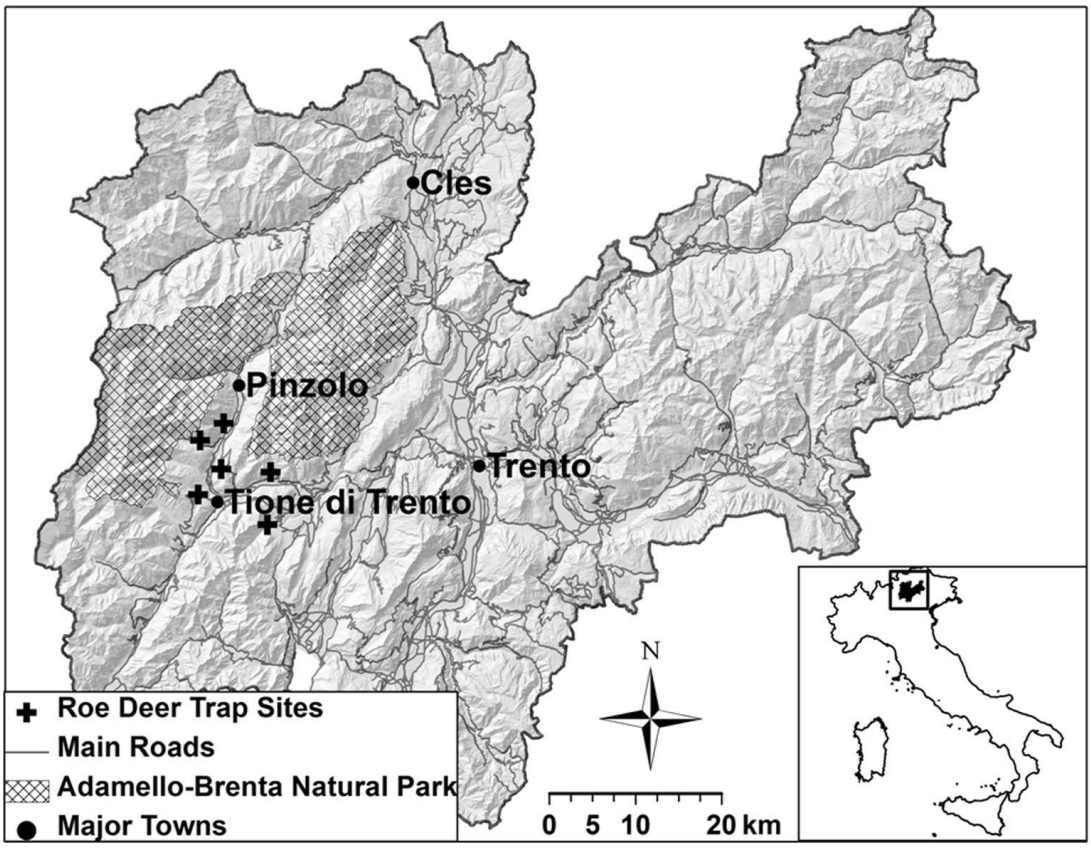


Figure 2- 1. Study area in the northwest of the Autonomous Province of Trento in northern Italy. We captured and deployed radio-collars on 22 roe deer (*Capreolus capreolus)* at five trap sites in winters 2012/2013 and 2013/2014.

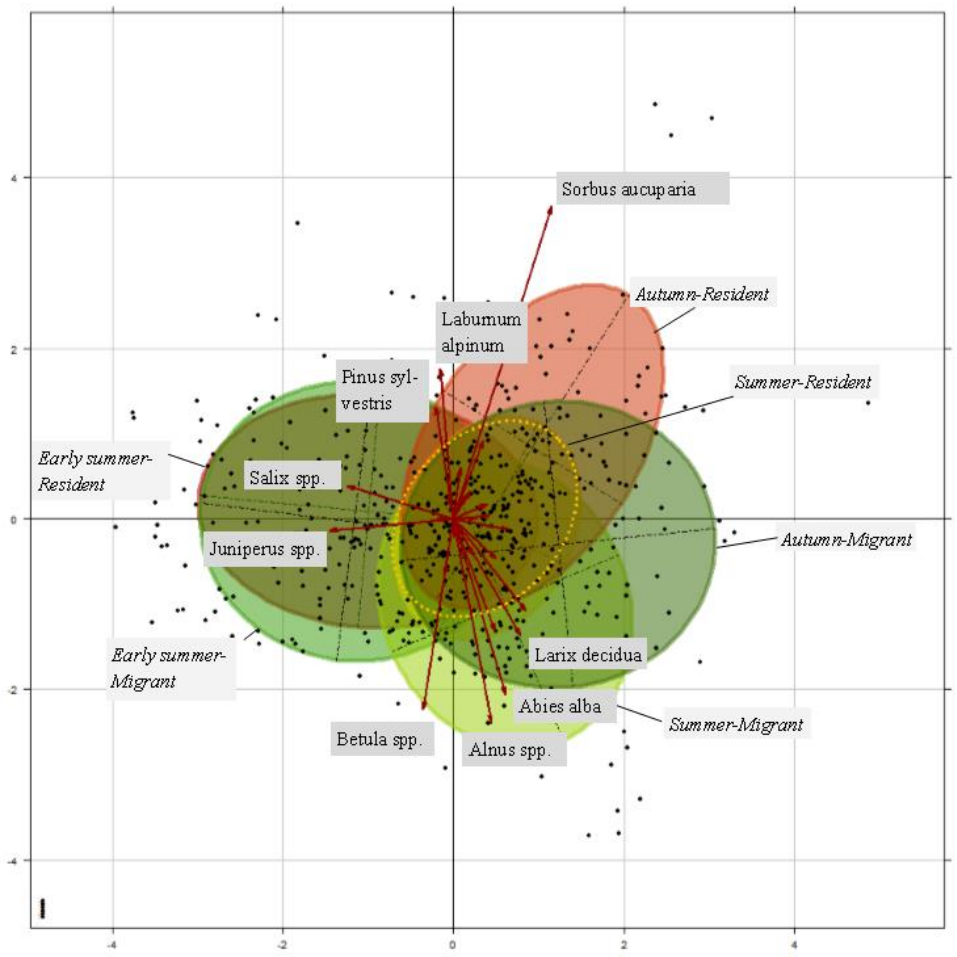


Figure 2- 2. Multivariate differences in overstory vegetation communities along movement trajectories of migratory (N=11) and resident (N=25) roe deer (*Capreolus capreolus*) in three time periods (early summer, ca. late April to mid-June; summer, ca. mid-June – mid-August; and late summer, ca. mid-August – late September) in two years (N_{2013}=14, N_{2014}=22). Column normed scores and class normed scores of the two axes from a Hill-Smith (HS)-between class analysis (BCA) based on cover characteristics including vegetation cover (%) and phenology classes (measured in 2 x 1m^2 quadrats) by plant groups (continuous variables) and overstory habitat types (characterizing the area around quadrats, ca. 50m radius; factor). For detailed information on sampling intervals see Appendix 2-B.

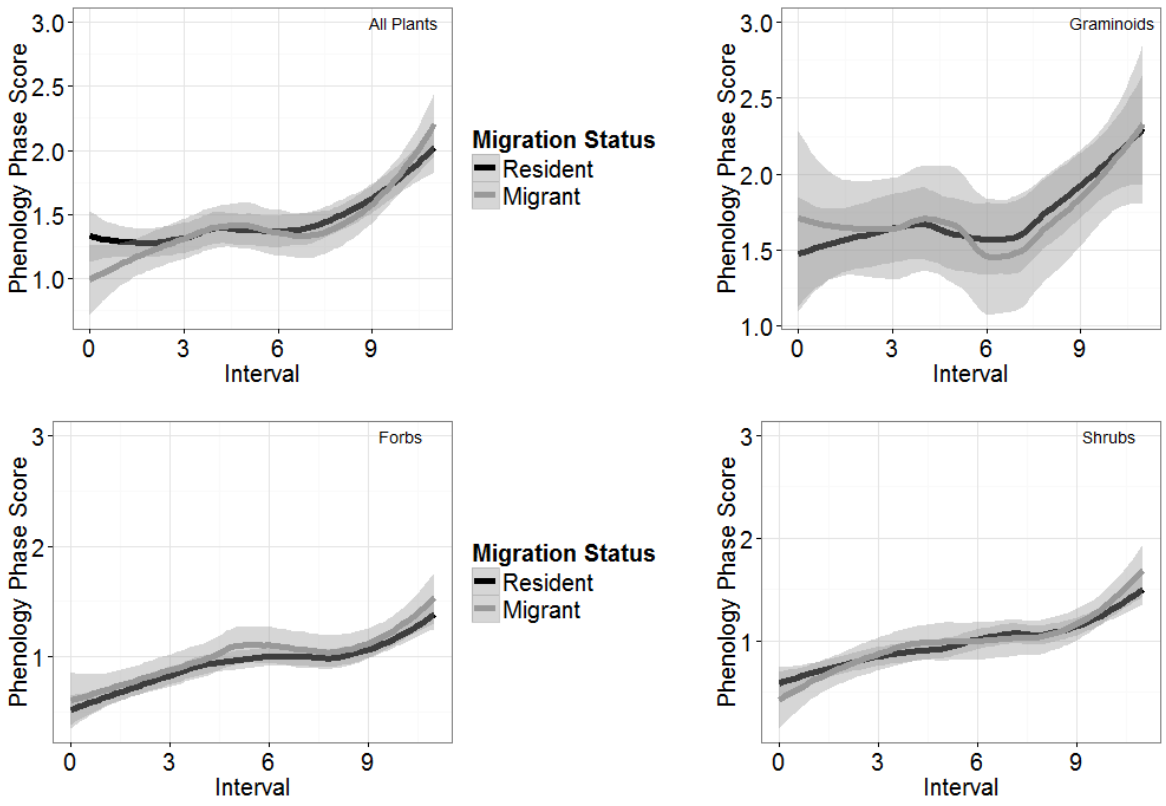


Figure 2- 3. Loess smoothed relationship (with 95% CI) between time (sampling interval) and frequency-weighted phenology scores (0-old, 1-newly emergent, 2-fruiting, 3-flowering, 4-mature, 5-cured) for all plants pooled, graminoids, forbs and shrubs measured along movement trajectories of resident (N=25) and migrant (N=11) roe deer (*Capreolus capreolus*) throughout the vegetative period in the northwestern Autonomous Province Trento, Italy. Sampling intervals represent 16-week periods starting in early April and ending in early October (e.g. interval 6 represents mid-summer from July 4th to July 19th). For detailed information on sampling intervals see Appendix 2-A.

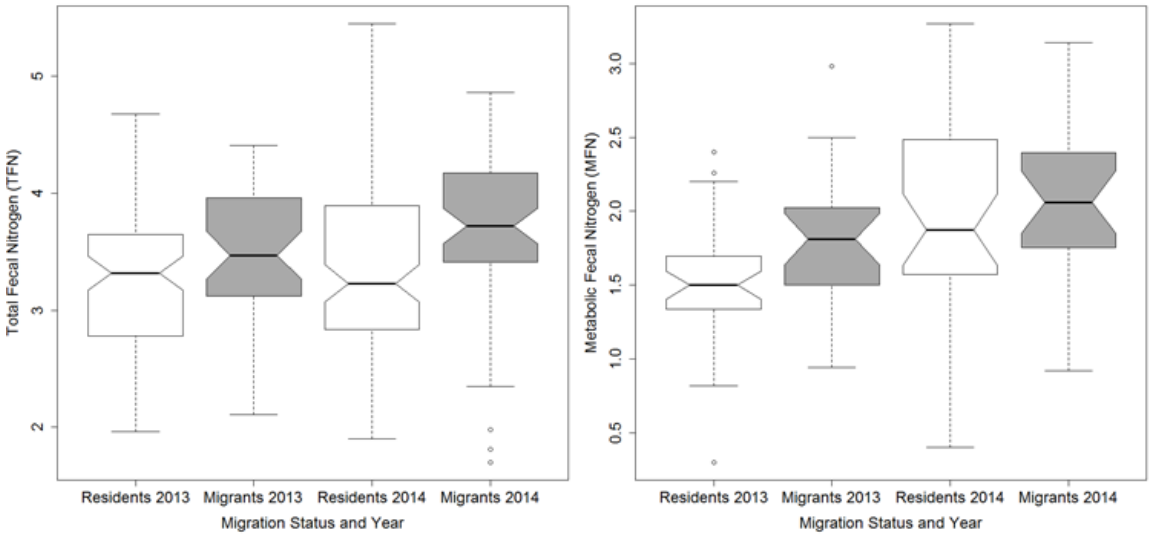


Figure 2- 4. Total fecal nitrogen (TFN) and metabolic fecal nitrogen (MFN), both in % organic matter, of roe deer (*Capreolus capreolus)* by migration status ($N_{residents}$=25, $N_{migrants}$=11) in two years (N_{2013}=14, N_{2014}=22, sampling unit was the roe deer sampling year). Fecal pellets were collected along movement trajectories throughout the vegetative period in the northwestern Autonomous Province Trento, Italy.

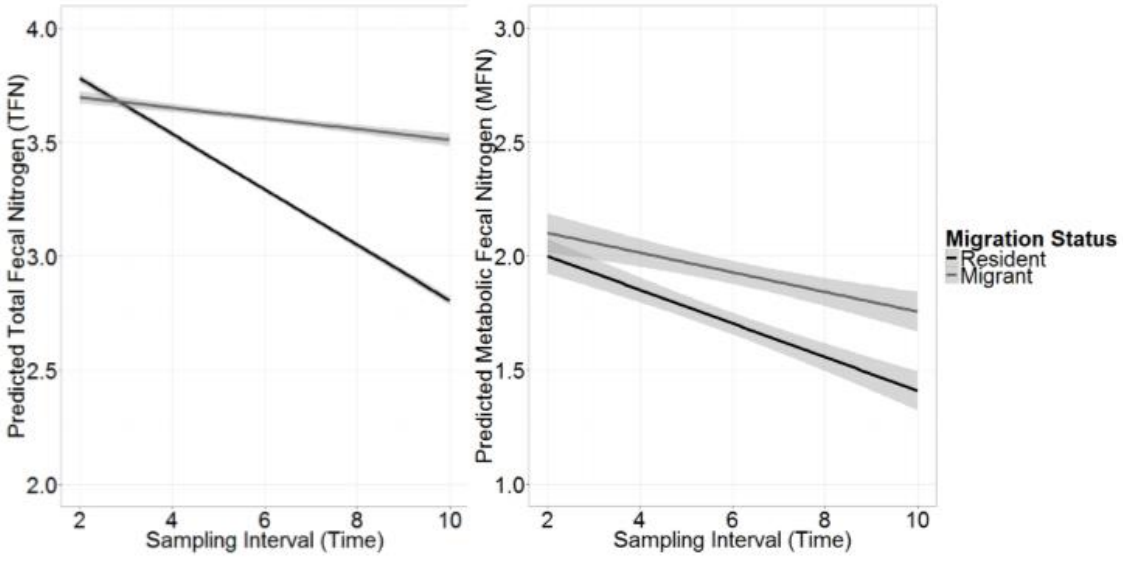


Figure 2- 5. Predicted total fecal nitrogen (TFN) and metabolic fecal nitrogen (MFN) from averaged linear models (with 95% CI) within two AICc. Models predict the relationship of TFN and MFN and predictor variables including sampling interval, migration status of roe deer (*Capreolus capreolus*), sex and sampling year. TFN (N=302) and MFN (N=118) were estimated from fecal pellets collected along roe deer movement trajectories of 25 resident and 11 migratory roe deer two years (N_{2013}=14, N_{2014}=22) throughout the vegetative period in the northwestern Autonomous Province Trento, Italy. Note the different scales on the y-axes. Sampling intervals represent 16-week periods starting May 9th and ending October 8th. We removed fecal samples collected during the first interval (before May 9th) due to artificial feeding of some roe deer during that period. For detailed information on sampling intervals see Appendix 2-A.

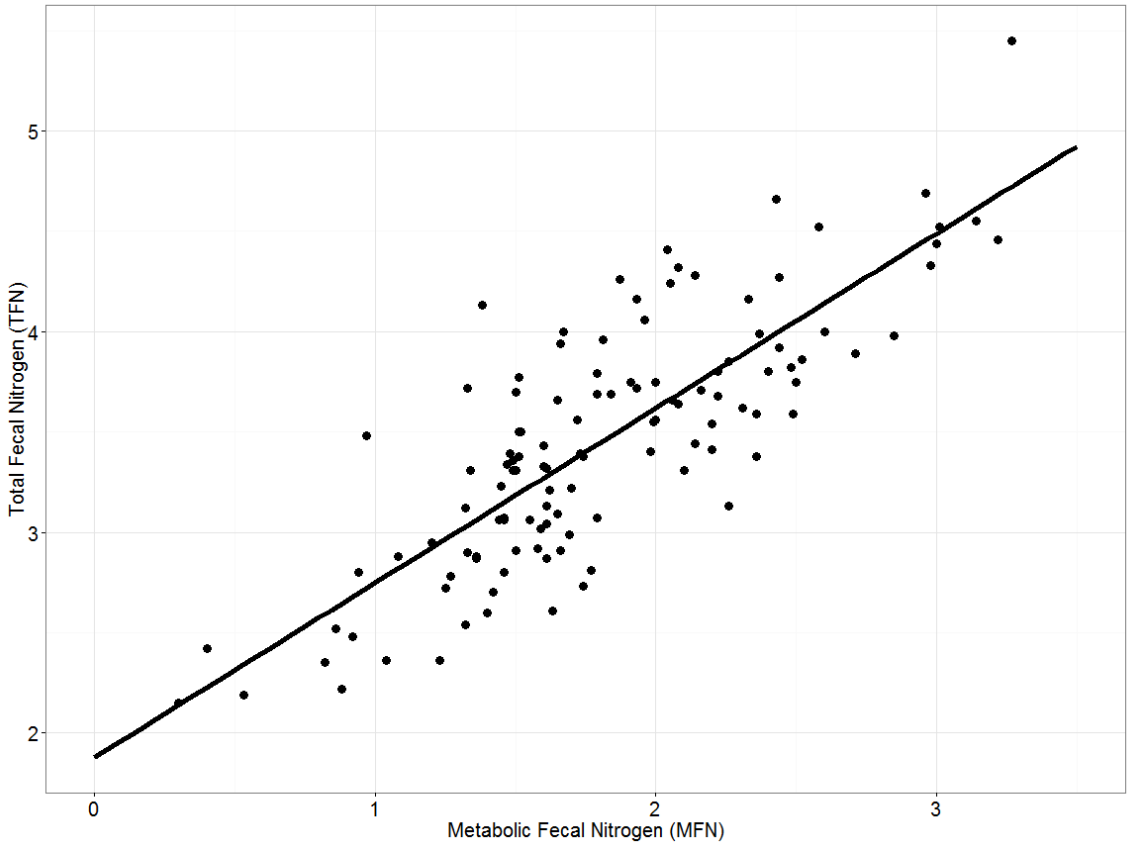


Figure 2- 6. Linear relationship between total fecal nitrogen (TFN) and metabolic fecal nitrogen (MFN), both in % organic matter, of roe deer (*Capreolus capreolus,* N=36) fecal pellets (N=118) collected along animal movement trajectories throughout the vegetative periods in 2013 and 2014 in the northwestern Autonomous Province Trento, Italy.

APPENDIX 2-A. Roe deer (*Capreolus capreolus*) capture information, monitoring year, migration classification (migrant = 1), sex (male (m), female (f)), age class (adult ≥ 2 years, yearling = 1 year, fawn < 1 year) and capture-site information. The global positioning collar (GPS) fix rate is given as proportion.

ID	Year	Mig-rant	Sex	Capture Date	Age	Fix Rate	Capture Site
2C2T32	2014	0	f	1/28/2014	Adult	0.77	Campidelli
2C2T34	2014	0	m	2/11/2014	Adult	0.99	Cerana
2C2T33	2014	0	f	1/28/2014	Fawn	0.81	Cioca
2C2T36	2014	0	f	2/11/2014	Fawn	0.86	Cioca
2C2T14	2014	0	f	1/25/2013	Adult	NA*	Credata
2C2T14	2013	0	f	1/25/2013	Adult		Credata
2C2T12	2014	0	m	1/23/2013	Adult	0.94	Credata
2C2T12	2013	0	m	1/23/2013	Adult		Credata
2C2T07	2013	1	f	12/20/2012	Adult	0.84	Croci
2C2T07	2014	1	f	12/20/2012	Adult		Croci
2C2T03	2014	1	f	12/18/2012	Adult	0.99	Iron
2C2T03	2013	1	f	12/18/2012	Yearling		Iron
2C2T08	2013	1	f	1/7/2013	Adult		Iron
2C2T08	2014	1	f	1/7/2013	Adult	0.99	Iron
2C2T02	2014	0	f	12/17/2012	Adult	0.95	Iron
2C2T02	2013	0	f	12/17/2012	Adult		Iron
2C2T39	2014	1	m	3/5/2014	Adult	0.74	Mortaso
2C2T11	2013	0	f	1/17/2013	Adult	0.98	Pandoline
2C2T11	2014	0	f	1/17/2013	Adult		Pandoline
2C2T37	2014	0	m	2/12/2014	Adult	0.89	Pra Cavai
2C2T25	2013	0	f	2/15/2013	Adult	0.98	Prà de Bert
2C2T25	2014	0	f	2/15/2013	Adult		Prà de Bert
2C2T26	2014	0	m	2/21/2013	Adult	0.86	Prà de Bert
2C2T26	2013	0	m	2/21/2013	Adult		Prà de Bert
2C2T23	2013	1	f	2/13/2013	Adult	0.99	Pulis
2C2T23	2014	1	f	2/13/2013	Adult		Pulis
2C2T27	2014	0	m	2/28/2013	Adult	0.92	Pulis
2C2T27	2013	0	m	2/28/2013	Adult		Pulis
2C2T09	2014	0	f	1/8/2013	Adult	NA*	Sostino
2C2T09	2013	0	f	1/8/2013	Adult		Sostino
2C2T29	2014	0	f	1/14/2014	Adult	0.91	Spiazzo Ricov.
2C2T24	2013	0	m	2/15/2013	Adult	0.97	Val Algone 02
2C2T24	2014	0	m	2/15/2013	Adult		Val Algone 02

Appendix 2-A continued

2C2T16	2013	0	f	1/29/2013	Adult	NA*	Val Algone 02
2C2T16	2014	0	f	1/29/2013	Adult		Val Algone 02
2C2T28	2014	1	m	1/13/2014	Adult	0.85	Val Marcia

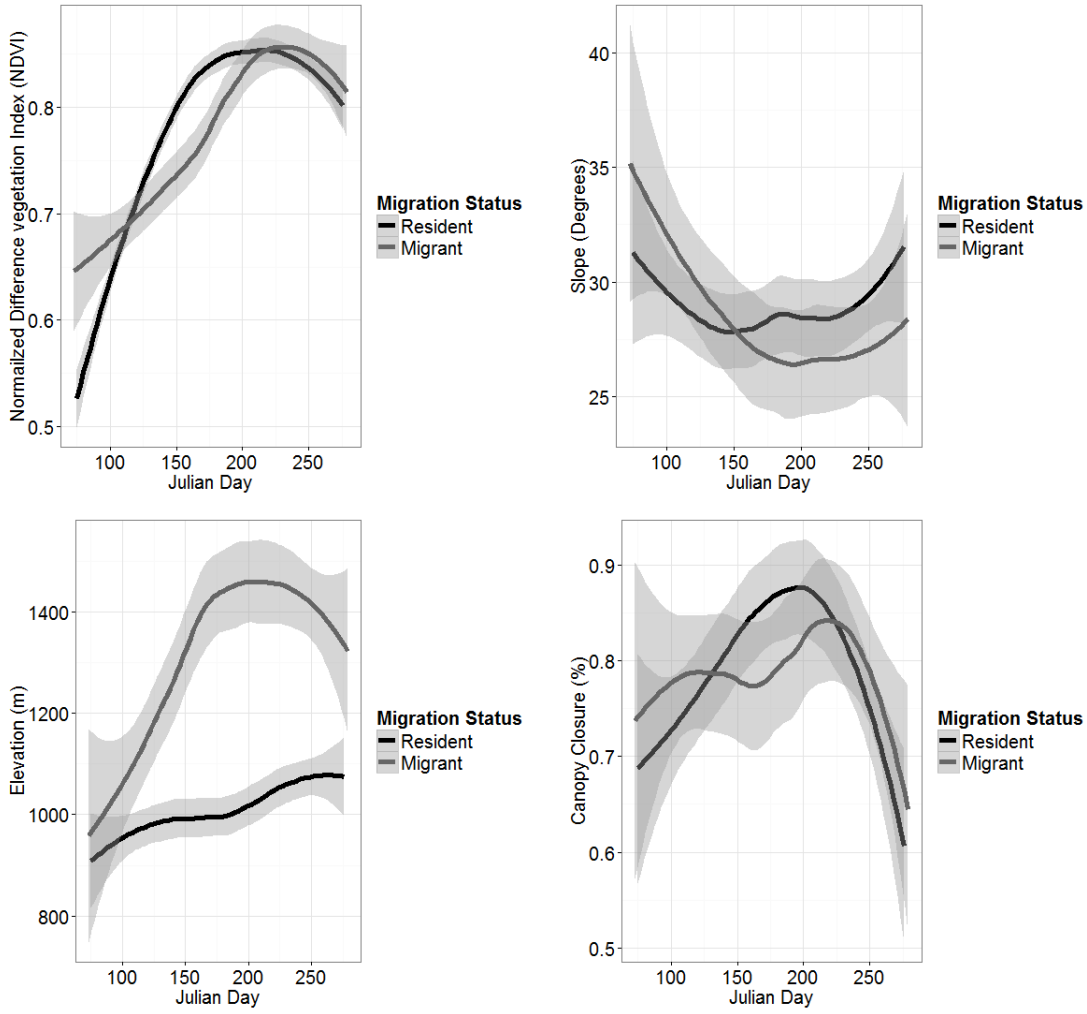
* Monitoring based on Very High Frequency (VHF) only

APPENDIX 2-B. Field sampling intervals for vegetation and fecal pellet collection along roe deer (*Capreolus capreolus*) movement trajectories during vegetation seasons in 2013 and 2014 in Val Rendena, Italy, and the intervals used to analyze pooled sampling data for a) plant phenology, b) fecal pellets and c) plant communities using between-class-Hill-Smith analysis (BCA).

Original Interval	a) Phenology	b) Fecal pellets	c) BCA	Begin	End
1a*	1	-	-	30-Mar	6-Apr
1b*	1	-	-	7-Apr	14-Apr
1c*	1	-	-	15-Apr	22-Apr
2	2	1	1	23-Apr	30-Apr
3	2	1	1	1-May	8-May
4	3	2	1	9-May	16-May
5	3	2	1	17-May*[1]	24-May*[1]
6	3	2	1	25-May	1-Jun
7	4	3	1	2-Jun	9-Jun
8	4	3	1	10-Jun	17-Jun
9	5	4	2	18-Jun	25-Jun
10	5	4	2	26-Jun	3-Jul
11	6	5	2	4-Jul	11-Jul
12	6	5	2	12-Jul	19-Jul
13	7	6	2	20-Jul	27-Jul
14	7	6	2	28-Jul	4-Aug
15	8	7	2	5-Aug	12-Aug
16	8	7	2	13-Aug	20-Aug
17	9	8	3	21-Aug	28-Aug
18	9	8	3	29-Aug	5-Sep
19	10	9	3	6-Sep	13-Sep
20	10	9	3	14-Sep	21-Sep
21	11	10	3	22-Sep	29-Sep
22	11	10	3	30-Sep	8-Oct

* Pilot sampling trials
*[1] No sampling in 2013

APPENDIX 2-C. Comparison of Normalized Difference Vegetation Index (NDVI), slope, elevation and canopy closure averaged on summer ranges of resident (N=25) and migratory (N=11) roe deer (*Capreolus capreolus*) in the north-west of the Autonomous Province Trento, Italy. Provided are the loess smoothed trends with their 95% CI of each variable over time (Julian day). Data were pooled for years 2013 and 2014.



CHAPTER 3. MIGRATION ACROSS THE HUTCHINSONIAN NICHE IN SPACE AND TIME BY A LARGE HERBIVORE[2]

INTRODUCTION

Animal movement in response to resource gradients can take many forms (Senft et al. 1987, Wiens 1989, Nathan et al. 2008). One much studied movement behavior is migration, which is classically defined as the seasonal movement of individuals from one region to another in response to spatiotemporal variation of resources (Southwood 1962, Fryxell and Sinclair 1988, Dingle and Drake 2007). 'Classic' long distance round-trip migrations, such as neotropical migratory songbirds or Serengeti wildebeest (*Connochaetes taurinus*), are the best known type of migration. Many of these well-known migrations take place at large spatial scales, but migratory movements may range orders of magnitude even within taxa (Hein et al. 2012). Consequently, migration can neither be described by its distance nor the characteristics of its routes (Cagnacci et al. in revision). For example, in large herbivores, seasonal movement distances may vary greatly as a function of spatiotemporal resource variability (Mueller et al. 2011, Teitelbaum et al. 2015, Peters et al. in prep [Chapter 4]).

Despite being a well-known and common ecological phenomenon, currently there is no unifying consensus on how to describe and define migration (Dingle and Drake 2007, Cagnacci et al. 2011, Börger and Fryxell 2012), but two commonly acknowledged concepts seem to separate residency from migration. First, migration is defined by the

[2] This chapter is intended for submission to Ecological Monographs. Authorship for this chapter includes W. Peters, M. Hebblewhite, F. Cagnacci, D. Spitz, S. Focardi, and other members from the Eurodeer group.

spatial separation (i.e. allopatry) of seasonal ranges (Southwood 1962, Dingle and Drake 2007, Fryxell and Sinclair 1988). Because spatial separation is a descriptive geographic measure, however, it does not explain the ecological mechanisms of migration. Second, migratory behavior is hypothesized to occur in response to *spatiotemporal resource variability* (Fryxell and Sinclair 1988). Differences in the spatial distribution of seasonal resources and their predictability are likely the main contributors to variation in seasonal movement (Fryxell et al. 2004, Mueller et al. 2011), but are often mediated by density-dependence (Lundberg 1988, Taylor and Norris 2007). In accordance with these characteristics of migration, the study of migration has tended to focus first on whether migration occurs or not (i.e., the pattern), and then, secondly, the determinants of migration (i.e., the process, Cagnacci et al. *in revision*).

A point of confusion in the study of migration is that seasonal movement is very flexible and seldom neatly fits into two categories of residency or migration, but rather occurs along a gradient between these two endpoints (Cagnacci et al. 2011, Cagnacci et al. *in revision*). Most animals display a behavioral plasticity of migration 'tendency' in response to spatiotemporal variability of resources (Cagnacci et al. 2011, Chapman et al. 2011, Sih et al. 2012). For example, landscapes that show very low spatial and temporal variation commonly support sedentary populations, while landscapes with high variability in space and time favor seasonal movements as direct proximate responses to changes in resource distributions (Jonzén et al. 2011, Mueller et al. 2011, Hein et al. 2012). With increasing seasonality and predictability, cue-driven migration, where animals migrate following seasonal stimuli, becomes more frequent (Sabine et al. 2002). In less predictable environments conditional migration, where animals migrate only

during certain years in response to environmental variation, may be expected (Nicholson et al. 1997, Sabine et al. 2002). This behavioral plasticity also leads to partial migration, when only a fraction of the population migrates and another remains resident either on the breeding or non-breeding range (Dingle and Drake 2007, Skov et al. 2011). Partially migratory systems provide an ideal model system for studying migration because of the explicit opportunity for comparisons of mechanisms driving the different migratory strategies (Chapman et al. 2011).

Just like formulating a unifying definition of migration, also agreement on measuring or classifying migration has not been achieved (McClintock et al. 2012). Consequently, classifying migratory behavior often depends on arbitrary rules that are often species-, taxa-, or study-area specific. Furthermore, classifications of migratory behavior, such as the net squared displacement (NSD; Bunnefeld et al. 2011, Börger and Fryxell 2012, Singh et al. 2012), the degree of overlap between seasonal home ranges (Mysterud 1999, Ball et al. 2001, Fieberg and Kochanny 2005) or spatial clustering of seasonal locations (Cagnacci et al. 2011, Cagnacci et al. *in revision*), are usually solely based on geographic space (i.e. the pattern). Uncertainty in geographic distance-based classification is often reported in animals that undertake multiple trips, have stop-over sites, do not stabilize in seasonal home ranges or undertake excursions (Cagnacci et al. 2011, Mysterud et al. 2011b, Bischof et al. 2012). Because changes of environmental conditions in space and time present the motivation to migrate (i.e., the determinants), Cartesian-based definitions of migration alone are insufficient to understand underlying processes of migration (Cagnacci et al. 2011; Cagnacci et al. *in revision*). Although several authors have emphasized that migration should involve moving between different

habitats (i.e., realized ecological niches) in space and time, to date this concept has not been used to measure, describe or define migratory versus non-migratory states. However, distances between seasonal ranges may be considered as horizontal distances, altitudinal distances, or even environmental distances (LeResche 1974). In fact, LeResche (1974) coined the term 'ecological distance', implying that migration involves movement across ecological gradients.

Ecological niche theory predicts that different species thrive within specific ranges of environmental conditions in distinct geographic ranges (Hutchinson 1957). The fundamental niche encompasses all *n*-dimensional combinations of abiotic factors in which a species can persist without immigration (Soberón 2007), while the realized niche represents the proportion that is actually occupied by a species in the presence of biotic factors, such as predation or inter- or intraspecific competition (Hirzel and Le Lay 2008). Density dependence is not only a common determinant for migration, but is also one main biotic determinants for limiting the realized niche in fundamental niche space (Soberón and Nakamura 2009). The dimensions of the realized niche can be estimated by measuring environmental conditions at geographic locations were animals are present. The geographic space inhabited by an organism depends on the distribution of environmental conditions in space and time (Pulliam 2000), but movement defines what geographic areas are accessible and thus, realized habitat (Soberón 2007). Consequently, movement is a critical dimension of the ecological niche through the lens of accessibility (Soberón 2007) and migration is an excellent example of the variation in the realized niche in time (Jonzén et al. 2011). Differential movement between geographically distinct 'niches' over time can be a critical component shaping the spatial distribution of species,

populations and individuals (Soberón 2007, Soberón and Nakamura 2009), and yet the relationship between the niche and migration has not been well understood.

One important question in the migration literature remains to what extent migratory individuals occupy similar niches throughout the year (i.e. niche following) or switch niches seasonally (Fig.3-1; Laube et al. 2015). The idea of niche following versus niche switching has been largely untested (Nakazawa et al. 2004, Jonzén et al. 2011), except in the avian literature (Jonzén et al. 2011, Laube et al. 2015). For example, in a comparative study of 21 migratory bird species, Nakazawa et al. (2004) found that the winter non-breeding season distribution of the Bell's Vireo (*Vireo bellii*) was predicted best by a model built with covariates describing the breeding-season, confirming that Bell's Vireo followed niches. In contrast, environmental conditions on the breeding range of the Magnolia Warbler (*Dendroica magnolia*) had very little explanatory power of its non-breeding winter range conditions, demonstrating niche switching between seasons (Nakazawa et al. 2004). Although understanding seasonal movement decisions requires knowledge of a species' ecological niche, the question of niche following versus niche switching has not been addressed for other taxonomic groups, including large herbivores.

Large herbivores offer an ideal taxonomic group of high ecological and economic importance (Hobbs 1996, Gordon et al. 2004) to study migration, especially because many migratory species are partially migratory, including impalas (*Aepyceros melampus;* Gaidet and Lecomte 2013), African buffalo (*Syncerus caffer*; Naidoo et al. 2012), Serengeti wildebeest (*Connochaetes taurinus*; Fryxell et al. 1988), moose (*Alces alces*; Ball et al. 2001), pronghorn (*Antilocapra americana*, White et al. 2007), red deer (*Cervus elaphus elaphus*; Mysterud et al. 2011, Peters et al. in prep [Chapter

4]), elk (*Cervus elaphus canadensis*; Hebblewhite et al. 2008), white-tailed deer (*Odocoileus virginianus*; Grovenburg et al. 2011) and roe deer (*Capreolus capreolus;* Cagnacci et al. 2011, Mysterud et al. 2011, Peters et al. in prep [Chapter 1], Peters et al. in prep [Chapter 4]). For ungulates, access to high quality forage in spring is thought to be the primary determinant of migratory behavior (Fryxell and Sinclair 1988, Hebblewhite et al. 2008). Ungulates migrate along seasonal gradients of forage quality, often also allowing individuals to reduce predation risk (Fryxell and Sinclair 1988) or mortality risk due to humans (Singh et al. 2012). Related to forage, migration is also a strategy to reduce density-dependent competition by migrating away from shared seasonal ranges (Fryxell and Sinclair 1988, Mysterud et al. 2011a, Middleton et al. 2013, Hopcraft et al. 2014). For example, Mysterud et al. (2011) and Eggeman et al. (*in revision*) tested the competition avoidance hypothesis in Norway and Canada, respectively, and showed that variability in the probability of migration was related to *Cervus spp*. density. Another study by Nelson (1995) indicted that white-tailed deer limited the time spent on shared winter ranges due to density dependent competition. Thus, environmental gradients in forage and predation risk and intrinsic gradients in density itself likely explain migratory behavior in ungulates (Fryxell and Sinclair 1988).

The overall aim of our paper is to test the efficacy of the ecological distance concept (LeResche 1974) to serve as a framework for understanding both the patterns (describing or measuring) and determinants (explaining the mechanisms) of migration in a large herbivore species with high behavioral plasticity (Fig. 3-2; Cagnacci et al. 2011). We evaluate the ecological distance concept using individual animal movement data from five populations from one of the most common ungulate species with a wide distribution

in Europe, the European roe deer (Melis et al. 2009). Roe deer occupy a wide range of habitats from northern Scandinavian boreal forests to Mediterranean chapparal environments (Linnell et al. 1998). Throughout the year, roe deer alternate between two main behavioral and physiological seasons: the reproductive season in spring and summer, when this species is mainly solitary, and the winter season, when small family groups can be observed (Hewison et al. 1998). A wide range of seasonal movement patterns have been documented within populations in northern environments (Wahlström and Liberg 1995, Mysterud 1999), in the Alps (Ramanzin et al. 2007, Peters et al. in prep [Chapter 2]) and between populations across Europe (Cagnaccci et al. 2011, Peters et al. in prep [Chapter 4]). For example, Cagnacci et al. (2011) and Peters et al. (in prep [Chapter 4]) found individual-level differences in migration probability as a function of winter severity and topography resulting in different proportions of migrants in five populations across Europe. Because roe deer display a high level of behavioral plasticity (Cagnacci et al. 2011), and many populations are partially migratory (Peters et al. in prep. [Chapter 4]), roe deer are an ideal model species for the study of migration.

We first tested whether individual roe deer occupied different realized seasonal niches (i.e. niche switching) to understand whether ungulate migration can be classified using ecological distance (e.g., describing the pattern and measuring migration, Fig.3-1, Question 1). Previous attempts to classify migration relied solely on geographic distance (Cagnacci et al. *in revision*). Here, we compare measures derived in both geographic space and ecological niche space. The last component of this first question entails that we combine geographic and niche ecological measures in an integrative framework to classify roe deer observations into groups along a continuum of migration tendency. If

roe deer track their niche over time, this predicts that there should be no relationship between geographic distances migrated, and niche overlap between seasonal niches (Laube et al. 2015). Alternatively, if roe deer switch niches while migrating, ecological and geographic distance should be correlated and ecological niches of migrants and residents should differ in summer. Second, we tested which environmental factors explained the differences between our migratory classifications at the level of the individual roe deer (mechanisms for migration, Fig.3-1, Question 2). Based on previous studies, we expected that differences in forage productivity should explain most variation in migration probability (Bischoff et al. 2012, Hebblewhite et al. 2008), and that these would be correlated with topographic variables (Mysterud 1999, Cagnacci et al. 2011; Fig 3-2, Question 2a). We finally tested the hypothesis that migratory behavior is dependent on spatiotemporal variation in resource availability and density at the level of the population to understand the broad-scale role of seasonality on migration (Fig.3-2, Question 2b). We predicted that the probability of migration in roe deer would be higher in more seasonal landscapes, but predictable (i.e. lower between-year variation) of forage resources. Further, we expected that decreased spatial variability of seasonal forage resources at the scale of the population should favor a lower prevalence of migratory behavior (Mueller et al. 2011). Both, temporal variability and the spatial variability of forage resources may be mediated by density with an overall higher probability of migration with increasing densities (Mysterud et al. 2011, Eggeman et al. *in review*).

METHODS

Study Areas and Animal Location Data

We used global positioning system (GPS) location data from 71 male and female adult roe deer in five European populations between 2005 and 2013 (Appendix 3-B) maintained by the collaborative Eurodeer project (Cagnacci et al. 2011; Fig.3-3). We did not include roe deer fawns, which may show dispersal behavior that could confound our analyses (Cagnacci et al. 2011). Our study areas included populations in Val Rendena, Italy (N=7, IT.1), Monte Bondone, Italy (N=11, IT.2), Bavarian Forest, Germany and Czech Republic (N=26, DE/CZ), Koberg, Sweden (N=14, SE) and western Norway (N=13, NO). Roe deer in these populations have been shown to be partially migratory, with fairly high migration rates with the exception of one contrasting population in Sweden with low migration rates (Cagnacci et al. 2011, Peters et al. in prep [Chapter 4]). Also, these five study areas represent a wide range of environmental conditions for partially migratory roe deer providing an ideal system to understand migratory plasticity and hypotheses across diverse systems. Animals were captured either with box traps or drive nets (Peterson et al. 2003). Animal care protocols were approved for each study population (e.g., University of Montana IACUC for Italy #AUP 060-12MHWB-113012). The GPS data sampling resolution ranged between 12 and 1 location/day and only 15% of the data had a sampling interval of 12 – 24 hrs, mainly due to missed fixes. Because the sampling interval differed within and between populations we standardized all animal location data and reduced the data to one daily average. This also helped to average away potentially significant observation error or missed fixes in the GPS location data. We considered an analysis year (i.e., 'migration year') to begin January 1st of year one and end

January 31st the following calendar year and included only animals that had daily averaged location data for at least 90% of this duration.

Relating Niche Theory to Migration

In Fig.3-2 we outline how we addressed our twin objectives of describing (the patterns) and explaining (the determinants) migration in roe deer. We first assessed the patterns of migration using geographic and ecological migration measures (Question 1 in Fig.3-2). Next, we estimated seasonal differences in ecological niche space by sampling the *n*-dimensional hypervolume (e.g. composed of climate, topographic, and forage parameters) at animal locations or occurrence sites during consecutive time periods (Hirzel and Lelay 2001). By measuring ecological conditions along the animal movement trajectories we aimed to test a) if roe deer realized niches change throughout the year (Fig.3-1) and if so, b) if these changes can be combined with geographic classification parameters to define the migratory continuum for roe deer with an integrative cluster analysis. We hypothesized that roe deer would switch seasonal niches rather then follow them, due to both their high degree of plasticity and seasonality. We next assessed the underlying ecological determinants separating different migratory behaviors identified using our integrative geographic and ecological approach at the individual- and population level (Questions 2a and 2b in Fig.3-2).

We chose environmental variables based on existing knowledge of ungulate and, in particular, roe deer migration and behavior. Competing hypotheses for seasonal ungulate movements, and habitat selection in general, commonly include topographic features, forage availability, landcover classification, and predation or human mortality risk (Fryxell and Sinclair 1988). Because these environmental covariates do not represent

mutually exclusive hypotheses and the variables are often correlated (e.g. forage quality and elevation), combining their effects in a generalized linear modeling framework is often statistically challenging (Hirzel and Le Lay 2008). Therefore, we took advantage of multivariate approaches that allowed inclusion of the effects of multiple competing hypotheses to explain ungulate movements, approximating the idea of the *n*-dimensional hypervolume (Fig.3-1; Hutchinson 1969). We next describe our specific methods and environmental variables.

Classification of Migration Plasticity (patterns)

Classifying Migration Plasticity in Geographic Space

We classified migratory behavior using two established pattern-based geographic methods for comparison to our process-based ecological niche measures (Question 1 in Fig.3-2). First, we used a spatially-explicit method that describes the outcome of the movement process by measuring the spatiotemporal overlap of seasonal animal locations (Cagnacci et al. 2011). We applied an approach developed by Cagnacci et al. (2011) to identify spatial separation of seasonal animal location clusters. We employed a supervised clustering procedure (SAS 9.2, PROC CLUSTER) to identify the two main non-overlapping location clusters of individual roe deer (herein spatial clustering method). This approach differentiates between residents versus non-residents. Migration distance was estimated with the Euclidian distance (km) between the centers of the seasonal location clusters.

Next, we used the net-squared displacement (NSD) method (Bunnefeld et al. 2011, Börger and Fryxell 2012) that applies competing non-linear models to the net squared displacement of an animal movement trajectory. The competing models

represent different seasonal movement types including residency, migration, mixed migration, nomadism and dispersal (see Bunnefeld et al. (2011) for a description of these movement modes). The best model was chosen based on the Akaike Information Criterion (AIC; Burnham and Anderson 2004). If more complex models were within two AIC we concluded that the additional parameter was uninformative and chose the simpler model (Arnold 2010). We excluded nomadism, because it is the movement type that is most commonly misclassified by this method due to its high variability (Bunnefeld et al. 2011). The distance between different seasonal locations was given by the asymptotic height of the top model (δ). For resident behavior δ remains approximately constant throughout the year, representing the average diameter of the home-range (Turchin 1998), while for migrants δ represents the square root transformed migration distance. NSD analyses were conducted in R 3.2.1 using the nls functions (R Development Core Team 2013). We restricted migration to a minimum residence time of 30 days on either seasonal range for both geographic methods (Cagnacci et al. 2011).

Classifying Migration Plasticity in Ecological Space

Next, we classified migratory behavior using a process-based ecological niche approach (Question 1 in Fig.3-2). Similar to our two geographic approaches above, we first used a measure to describe the separation of seasonal ecological niches (conceptually comparable to the spatial separation of animal location clusters). Second, we measured ecological 'movement' throughout the year in environmental niche space (conceptually comparable to the NSD). We first tested if there was ecological separation between seasonal niches of migratory roe deer (Fig.3-1) using Schoener's D (Schoener 1974) as a quantitative measure of niche overlap comparing the niche extents of the first winter

(January - March) to the summer (June – August) based on methods described by Broennimann et al. (2012). We applied kernel smoothers to densities of animal locations and associated environmental variables collected in geographic space to create a gridded multivariate ecological niche space and estimate Schoener's (realized) niche overlap (range between 0 and 1). We calculated the density of occurrences and their associated environmental variables collected at seasonal animal locations along the environmental axes of a multivariate Hill and Smith Analysis. We did not correct the occurrence of each species by availability of their environment (i.e., used only design; Broennimann et al. 2012). Then, we measured niche overlap along the gradients of this multivariate analysis. We calculated kernel density functions to derive the smoothed density of location occurrences as a function of the seasonal environmental covariates for each individual and projected that onto a gridded multivariate ecological space (Broennimann et al. 2012). We calculated niche overlap between the two seasonal ranges on the occupancy values in the summer and winter grids. For this analysis we adapted R code provided by Broennimann et al. (2012).

Next, because we wanted to track the niche space through which an individual roe deer traveled throughout the year, we estimated the ecological distance (ED) between consecutive daily locations of individual roe deer, that is, the ecological realized niche of each individual through time. We sampled environmental covariates at daily animal locations (see Environmental Covariates below) and applied a multivariate Hill and Smith Analysis to these daily animal location data for each individual separately (R-package 'ade4'; Chessel et al. 2004). The Hill and Smith method allows to incorporate continuous and categorical environmental variables to represent the *n*-dimensional

environmental realized niche space. To understand whether there was movement in the seasonal niche throughout the year (e.g., to estimate the ecological distances roe deer travel), we grouped animal locations by month for every individual and used a Between-Class Analysis (BCA) on the Hill-Smith standardized scores by accounting for the effect of the "month" as a factor (Doledec and Chessel 1987). All variables were standardized and we selected the number of axis for each analysis by screening screeplots for an 'elbow effect' to determine the number of axes to retain in the analysis (Jongman et al. 1995). For each individual, we measured the niche positions of all animal locations (i.e. the class coordinates from the BCA). Centered on the first observation for an animal of the year considered, this allowed us to track the movements in niche space as a function of the environmental covariates considered. Next, we extracted different parameters (see below) from these environmental niche trajectories.

We plotted the coordinates of BCA axis 1 and axis 2 and treated them as coordinate data in niche space. Using the same methods that we used to estimate the NSD following Bunnefeld et al. (2011), we fit non-linear models to these environmental niche trajectories and selected the model with the best fit based on AIC. Similar to how we measured Cartesian migration distance using the geographic NSD method, we estimated the ecological distance (ED, niche position) of individual roe deer seasonal movements by the asymptotic height of the top model (δ). Because migration may be described best by a variety of different measures (Cagnacci et al. *in revision*) of ED, we derived several parameters, including the relative change in ecological distance (change in niche position) between the starting month (always starts at 0 distance) and the average of the

summer months (June, July, August; herein $ED_{wi\text{-}su}$) and the standard deviation during the summer ($ED_{SD;}$ a measure of seasonal niche stability or niche breadth).

Towards an Integrative Approach to the Classification of Migration Plasticity

We compared geographic and ecological classification approaches individually, but then combined them in an integrative approach to classify roe deer along the migration continuum (Cagnacci et al. 2011). We used k-means cluster analysis to compare how much variation was explained in classifying seasonal movements by roe deer by the three classification systems; geographic space, ecological space and our integrative approach, and which approach provided the most parsimonious number of categories. For geographic space, we performed cluster analysis on the distance between seasonal geographic clusters, the δ of the NSD, and the categorical classification from each geographic method (i.e. resident or migrant for the spatial clustering method and four categories defined by NSD: migrant, resident, mixed migrant, dispersal). For ecological space, we included the δ of the ED, the niche overlap (D), the $ED_{wi1\text{-}su}$, the ED_{SD} and the four categories defined by ED: migrant, resident, mixed migrant, dispersal, in the k-means cluster analysis. For our integrative classification approach we conducted a k-means cluster analysis on all geographic and ecological measures combined. For each combination of measures we created a dissimilarity matrix between the observations using the Gower's distance (Gower 1971), allowing us to include categorical and continues predictor variables. For each approach, geographic, ecological and integrative, we estimated the natural number of clusters using the optimum average silhouette width (Rousseeuw 1987). The silhouette describes the tightness and separation of the data points within a cluster. The average silhouette width ($\bar{s}(k)$) of all clusters provides an

evaluation of the clustering validity and can be used to define the number of clusters maximizing separation. Cluster analyses were conducted using the R package 'cluster' (Maechler et al. 2015).

Determinants of Migration Plasticity

Determinants Underlying Seasonal Niches of Individual Roe Deer

We tested our hypotheses regarding the determinants of migration plasticity at the individual- (Question 2a) and the population- (Question 2b) level using the integrative (see *Results*) approach developed above to describe and classify seasonal migration behavior. We first used canonical discriminant analysis (DA) in R-package 'ade4' to test the hypothesis that a combination of forage resources, topography and risk separate niches of roe deer with different seasonal movement strategies during winter and summer (Question 2a; ter Braak 1995). We averaged a suite of standardized environmental variables (see below, Appendix 3-B) measured at GPS locations (realized niche) of individual roe deer for winter (January – March) and summer (June - August). Groups for the DA were defined by the clusters identified using the integrative classification (see *Results*) and the two seasons. Here we consider the distribution of the groups along the gradients as a function of environmental variables as the realized seasonal niches. We used Monte Carlo permutation tests to assess the statistical significance of the DA (999 permutations, $\alpha = 0.05$; ter Braak 1992). Finally, we produced a biplot to represent the different groups of migration strategies and seasons and environmental covariates in realized niche space and reported canonical coefficients (CC) to assess the influence of environmental variables in discriminating the groups.

Determinants for Population-level Differences in Migratory Probability

Next, to test the hypothesis that migratory probability (defined by our classification) was a function of spatiotemporal variability in forage resources, mediated by density, we used generalized linear mixed-effects models (GLMM). We considered random effects for study area to control for repeated observations within our five populations and differences in the number of roe deer sampled (Gillies et al. 2006). We tested for the effects of density, overall predictability, seasonality and inter-annual variation of forage resources as well as their spatial variation using contingency (seasonality) and constancy (inter-annual variability) and their standard deviations (SD) across all individual animal GPS location data (see *Environmental Covariates* below). We predicted that landscapes with lower temporal and/or spatial resource variation have lower probabilities of migration. We also predicted that migratory probability would increase at higher densities under the competition-avoidance hypothesis (Mysterud et al. 2011). We used the Analysis of Deviance (ANODEV) method to quantify the amount each variable accounted for in migration probability (Grosbois et al. 2008). The ANODEV compares the deviance of three models including the basic intercept model, an intermediate model and a more complex model. The R^2 of the ANODEV measures the proportion of variation in migration probability that is accounted for by each additional variable. Our intermediate model included only population density reclassified into three continuous categories, where low densities included 0-1.5, medium densities included 1.5-3 and high densities included >3 roe deer/km^2. The complex model included the variables describing temporal variation of forage resources or their spatial variation measured as SD across all annual locations of individuals within each population. We

transformed nonlinear covariates upon visual inspection and screened all covariates for collinearity using the Pearson's correlation coefficient threshold of $| r | > 0.6$ (Hosmer and Lemeshow 2000). We chose our top model based on the Akaike Information Criterion for small sample sizes (AICc, Burnham and Anderson 2002).

Environmental Variables

We used a suite of environmental resource variables to describe realized niche dimensions at used roe deer locations using static and dynamic variables for each individual daily location. All variables, their resolution and their use for our specific research questions are listed in Appendix 3-B. Forage availability is often described using remotely sensed vegetation indices such as the Normalized Difference Vegetation Index (NDVI) and large herbivore migration and movements have been shown to be strongly correlated with NDVI (Hebblewhite et al. 2008, Bischof et al. 2012, Morellet et al. 2013). We used MODIS satellite NDVI raster layers with at temporal resolution of 16-days and a spatial resolution of 250 m. NDVI data were smoothed using methods described by Maselli (2004). We calculated the SD and average NDVI during the growing season for which we used nine 16-day NDVI composite rasters between May 9th and September 14th during ordinary years and May 8th and September 13th during leap years. Further, topography has been shown to affect seasonal movements of ungulates, including aspect (Mysterud et al. 2011), slope (Cagnacci et al. 2011) and elevation (Albon and Langvatn 1992). We used digital elevation models (DEMs) from which we derived elevation, slope, ruggedness and aspect. We characterized land-use with the EEA-Corine Landcover Classification (CLC) 2006 and grouped individual landcover types into eight classes (Appendix 3-

B). Escaping risk due to predation and human caused mortality is another one of the main hypotheses to explain migration (Fryxell and Sinclair 1988). Although we did not have a direct measure of human or predation risk, we used proxies to characterize overall risk for roe deer. We described human activity using the night light index (Small et al. 2005, Morellet et al. 2013) and risk exposure using canopy closure (Hansen et al. 2013), because previous studies showed that roe deer sought dense cover to escape or reduce risk of predation (Mysterud and Ostbye 1995, Lone et al. 2014). Roe deer densities were estimated with different methods across our five study areas including fecal pellet distance sampling, infrared camera distance sampling and hunting bag estimates (see Appendix 3-A for more information). Because of the challenge of combining different methods across study areas, we classified roe deer into a new continuous density variable to describe low (1), medium (2) and high (3; as described above).

Upon classifying migration behavior we explored the determinants of the different migration strategies. We used synthetic variables in addition to those described above that have been hypothesized to affect the probability of migration (Fig.3-2). These variables included contingency, constancy and predictability of NDVI (Colwell 1974), which measure seasonality, between-year variability and overall predictability of forage resources. We produced spatial rasters of contingency and constancy following methods described by English et al. (2012) based on Colwell (1974) using the same smoothed NDVI data as above with a 250m spatial and 16-day temporal resolution. NDVI data were collected between 2000 and 2014. In the case of complete constancy, NDVI would remain the same in all seasons and all years, while

in the case of complete contingency NDVI would show seasonal patterns that are the same for all years (Colwell 1974). We also calculated the SD of contingency, constancy and predictability as a measure of spatial variation of forage resources. All measures of spatiotemporal forage variation differed between the five study areas (Fig.3-3). Lastly, climate has been shown to affect seasonal ungulate movements (Nicholson et al. 1997, Ball et al. 2001, Cagnacci et al. 2011). We used a winter severity index, the average annual temperature and the average temperature of the warmest quarter to characterize the overall climate at roe deer occurrence sites (Hijmans et al. 2005; Appendix 3-B). Prior to each analysis, we screened variables for outliers and considered log-transformations for continuous variables when relationships between variables appeared to be non-linear.

RESULTS

Classifying Migration Plasticity in Geographic and Ecological Space

We found both similarities and differences in the classification of migratory behavior using geographic and ecological approaches (Table 3-1, 3-2). In general, the two geographic measures yielded similar results in terms of distances of seasonal locations (Table 3-2). For example, migration distance measured by δ from the NSD and the distance between seasonal geographic clusters from the spatial clustering method correlated with r=0.98. But, when comparing the classification by the two methods we found substantial differences in classifications (Table 3-1). To facilitate the comparison of classifications between the NSD and the spatial clustering, we combined migrants, mixed migrants and dispersers versus residents identified with the NSD, because the spatial clustering method does not differentiate between movement

types with more than one annual range. We initially removed fawns from the data to not confound migration with dispersal (see methods; Cagnacci et al. 2011), therefore the high proportion of dispersers identified (up to 27%, Table 3-2) by the NSD method was surprising. Because we excluded age classes that are known to disperse, we believe that the 'dispersers' identified here were most likely misclassified migrants (mixed or otherwise) misclassified (e.g., Bunnefeld et al. 2011). The lowest agreement between the two geographic based methods was found in Sweden (SE; Table 3-1). Here, the NSD classified 71% of the roe deer as migrants (i.e. here sum of migrants, mixed migrants and dispersers), while the spatial clustering identified only 14% as migrants, although NSD mainly found mixed migration and no animal was classified as a clear migrant. Highest agreement was found in the Italian Monte Bondone population (IT.2), where the spatial clustering identified 73% as migrants and the NSD 82%.

When comparing the classification of the geographic migration measures and our ecological migration measures we found highest classification agreement for the German/Czech roe deer population (DE/CZ). For example, using the NSD method 15% of all DE/CZ roe deer were classified as migrants, 42% as mixed migrants, 35% as residents and 8% as dispersers. Using ED 8% were clear migrants, 50% were mixed migrants, 38% were residents and only 4% were classified as dispersers. The average niche overlap between winter and the following summer was 39% in the Italian Val Rendena (IT.1) population, 42% in the Italian Bondone (IT.2) population, 54% in Norway (NO), 50% in Bavaria (DE/CZ) and 62% in Sweden (SE; Fig.3-4). The negative relationship between niche overlap and geographic migration distance in

km from NSD (r = -0.57; Fig.3-4) confirms that migratory roe deer switch niches rather than follow them. The δ from ED increased with δ from NSD (r = 0.50) and the δ from ED was negatively correlated with niche overlap (r = -0.58).

Integrative Classification of Migratory Plasticity

The optimal number of clusters determined for the measures of the geographic space was 12 with the maximum discrimination ability of a silhouette width of 0.86 (Fig. 3-4). This indicates that there was a very clear structure to the clusters, with most observations seeming to belong to the cluster that they were assigned to (Rousseeuw 1987). Overall though, the 12 clusters identified seemed to correspond to differences in individual movement strategies within the 5 populations. Using our ecological measures only, an average silhouette of $\bar{s}(k) = 0.45$ was achieved with three clusters, which loosely represented migrant, resident and an intermediate strategy. A $\bar{s}(k) = 0.45$ indicates that there was a structure identified in the data, but not as strong as the geographic approach. A silhouette of 0.51 (indicating that a reasonable structure has been found) was achieved with only two clusters (migrant, resident) for the integrative approach, which combined all measures of geographic and ecological space (Fig.3-4). Although geographic measures found a stronger structure, the integrative combination of ecological and geographic measures provided a much more parsimonious explanation of variation in migratory behavior of roe deer. Lastly, the high variation within and between the approaches based on geographic and ecological space encouraged us to use their combination as most appropriate to address our second major question (Fig.3-2) on the mechanisms explaining migration.

Based on the integrative classification, the first of our two clusters (herein C_R, N=53) contained more animals showing characteristics of residents animals (e.g. 75% according to the spatial clustering method, Table 3-2), while the second cluster (herein C_M, N=18) captured migratory animals (e.g. 100% were migrants according to the spatial clustering method; Table 3-2). The $\bar{s}(k)$ of C_R was 0.55, while the $\bar{s}(k)$ of C_M was 0.48. Both clusters showed differences in their average geographical and ecological migration measures, where individuals classified in C_R had smaller average Cartesian and Ecological distances and seasonal location and niche overlap values (Table 3-2).

Determinants Underlying Seasonal Niches of Individual Roe Deer

The permutation test of the discriminant analysis indicated that the four groups (i.e. the combinations of two-season and two-class migratory status) were significantly different ($P < 0.01$). While both seasonal niches of residents indicated a high degree of similarity in environmental covariates, the biplot (Fig.3-6) showed a distinct separation of the seasonal niches for C_M. The first discriminant component (DS 1), which contributed 54% to the variance explained, mainly separated the seasonal niches of the migrant cluster from both seasonal niches of the resident cluster. Both seasonal niches of migrants were associated along this first component. In contrast, the second discriminant component (DS 2), which contributed 46% to the variance explained, mainly separated the summer niches C_M from the winter niches of both residents and migrants (Fig.3-6, Table 3-3). Environmental variables that were negatively correlated with DS 1 were associated with C_M and environmental variables positively correlated with DS 1 were associated with C_R. In contrast, environmental variables that were negatively correlated

with DS 2 were associated with summer niches and environmental variables positively correlated with DS 2 were associated with winter niches.

Environmental variables discriminating both seasonal migrant niches from resident niches indicated that resident roe deer were characterized by lower SD in NDVI (DS1= -0.80), lower elevations (DS1 = -0.55), less steep slopes (DS1 = -0.48) and less rugged habitat (DS1 = -0.40). Next, variables explaining differences between winter and summer niches, especially of migratory roe deer, included winter severity (DS2=-0.51), elevation (DS2 = -0.44), % agriculture in seasonal ranges (DS2 = -0.41) and constancy of NDVI between years (DS2 = 0.41). In general, variables that were mainly associated with summer niches of migrants (i.e. negative on DS1 and DS2) were elevation (DS1=-0.55, DS2= -0.44), seasonality (contingency; DS1= -0.27, DS2= -0.38) and the proportion of conifer within summer ranges (DS1= -0.24, DS2 = -0.37). Winter niches of migrants (i.e. negative on DS1 and positive on DS2) were mainly associated with slope (DS1= -0.48, DS2 = 0.21) and ruggedness (DS1= -0.40, DS2=0.26, Fig.3-6). In contrast, winter niches of residents (i.e. positive on DS1 and DS2) showed highest association with average NDVI within their winter ranges (DS1= 0.52, DS2 = 0.09) and higher canopy closures (DS1= 0.17, DS2=0.24). Summer niches of residents (i.e. positive on DS1 and negative on DS2) were mostly associated with agriculture (DS1= 0.03, DS2 = -0.41; Fig.3-6, Table 3-3). However, associations were much weaker for resident niches than for migrant niches.

Determinants for Population-level Differences in Migratory Probability

As hypothesized, the probability of migration increased with density (Table 3-4, Fig.3-7). The probability of migration also increased with overall predictability of the

NDVI and seasonality (i.e. contingency) of forage resources, while it decreased with increasing constancy (lower between-year variation) of forage resources. However, the p-values of contingency, constancy and overall temporal predictability, characterizing temporal variation were not significant at alpha ≤ 0.05 and the proportion of variation in migration probability that these variables accounted for was low ($R^2_{ANODEV} = 0.07 – 0.21$). The probability of migration increased for variables incorporating temporal and spatial variation (Fig.3-7). All three variables characterizing spatial variability (i.e. the SD of contingency, constancy and predictability) were statistically significant and accounted for a high proportion of the variance in migration probability ($R^2_{ANODEV} = 0.49 - 0.50$). The model with the lowest AICc described migration probability as a function of increasing density and increased spatial variability in seasonality (contingency). Interactions between density and variables characterizing spatiotemporal variation were not statistically significant. Lastly, we found no significant random effect for study area when including random effects in our top model (Var. = 0.668, SD = 0.817, AICc = 69.14) and therefore used fixed effects only.

DISCUSSION

We applied a conceptually novel and integrative approach to classify migration and assessed the determinants for different seasonal movement strategies using the example of a large herbivore with high ecological plasticity. We addressed the link between individual migratory movements and the environment in which they occur. As hypothesized, migration patterns of roe deer, evidenced through the ecological distance analysis and the relationship between geographical migration distance and niche overlap (Fig.3-4), indicated that migratory animals move to different

environmental niches (i.e. switch seasonal niches), while residents largely remain within the same niches year around. We were able to use the migration measures estimated in ecological space and combine them with geographic classification measures to achieve a more integrative classification of migration plasticity (Question 1). Next, the results of our second research question confirmed that many of the drivers of migration reported in other large herbivore species also applied across five roe deer populations in this study. Our work contributes to the understanding of drivers for roe deer migration. Interestingly, roe deer seasonal movement plasticity has not been studied much besides being a very well-studied species (Cagnacci et al. 2011). In particular the determinants for individual migration propensity appeared to be a multi-causal (Mysterud et al. 2012) function of forage availability and variability, terrain and climate. Finally, we also confirmed the importance of the competition-avoidance hypothesis and spatiotemporal variation in forage resources (resource seasonality hypothesis) for driving roe deer migration across Europe. At the population level, roe deer were more likely to avoid competition as density increased, and also were more likely to migrate in more spatially variable seasonal environments.

Classification of migration is a key step before being able to test hypotheses about migration. However, like finding a unifying definition for migration (Dingle and Drake 2001), classifying seasonal movement strategies has been a much-discussed problem in ecology (Cagnacci et al. *in revision*). Movements are usually categorized using geographic methods only, although distances between seasonal ranges may be considered as horizontal as well as altitudinal or environmental

distances (LeResche 1974). Consistent with a growing number of recent studies, we found substantial variation in the classification of roe deer movement strategies using common geographic measures. For example, Cagnacci et al. (*in revision*) found that consistency between three classification methods based on geographic space was only 50% and no method clearly outperformed another. Individuals falling towards the endpoints of the migration continuum (i.e. clear residency or clear migration; Cagnacci et al. 2011) were usually classified consistently between methods in our and previous studies (Cagnacci et al. *in revision*). In contrast, individuals displaying equivocal movement strategies (e.g. with multiple trip migrations or overall low range fidelity), commonly observed in partially migratory populations, showed substantial disagreement between methods.

The NSD method has recently become the standard for classification of migratory behavior especially for mammals. However, it is often applied in combination with other methods, visual inspection of movement trajectories or arbitrarily defined thresholds (Mysterud et al. 2011, Bischoff et al. 2012, Cagnacci et al. *in revision*, Eggeman et al. *in revision*). When applying the NSD method to simulated data, Bunnefeld et al. (2011) found high agreement between the simulated patterns and the NSD classification results for mixed migration, migration and dispersal. However, the NSD method misclassified 58% of all simulated individuals displaying resident behavior and interestingly, misclassifications of residents were commonly identified as dispersers (Bunnefeld et al. 2011). This suggests that resident strategies may be underestimated in studies using this method without applying additional measures, such as a minimum distance moved (Eggeman et al. *in revision*),

or visual inspection of trajectories. Indeed, the NSD method also identified a high proportion of dispersers in our dataset, which was surprising, because we only used data from adult roe deer and dispersal is commonly expected in juveniles (Wahlström and Liberg 1995). Consistent with these potential criticisms of the NSD method, our integrative approach discriminated higher proportions of residents in all study populations compared to the geographic and ecological classification methods alone (Table 3-1). Because true migration status was not determined and data were not simulated, we cannot strictly recommend one approach over another.

Migratory plasticity is one of the main reasons why unambiguous classification is so difficult (Cagnacci et al. *in review*). For highly plastic roe deer the integrative classification approach was the most parsimonious (identifying two strategies) while linking spatial and environmental niche patterns. The clusters based on geographic measures likely identified each individual population-specific strategy (Table 3-1), reflecting the highly diverse gradient ranging from perfect residency to perfect migration (Cagnacci et al. 2011). However, this is a clear example of statistical overfitting that undermines attempts to understand the generality of migration. Because of the high parsimony achieved by our integrative approach, we think it has great merit in the study of partially migratory behavior and was especially suitable for the questions addressed following our classification.

The ecological niche of a species has often been considered a static entity (Franklin 2010). But environmental conditions, and thus niche space in which animals exist, are dynamic in space and time (Jonzén et al. 2011). The general idea of niche

following versus niche switching is a largely unexplored aspect in understanding the diversity of migratory systems (Nakazawa et al. 2004). Niche switching versus niche following may be a function of the plasticity of a species as well as the habitat individuals live in (Laube et al. 2015). Individuals that follow the same environmental niche throughout the year may be more adapted to conditions or resources that are expected under a constant resource regime, while individuals that switch make a quantitative switch between the seasons. For neo-tropical bird species, Nakazawa et al. (2004) found that most species followed a particular niche throughout the year, whereas some species clearly switched niches between seasons. We present one of the first studies addressing whether ungulates switch or follow niches and for the highly plastic roe deer, we found that migrants switch their seasonal niches. The reasons for niche switching may be multifaceted, including deteriorating environmental conditions or density-dependence (Taylor and Norris 2007) restricting the realized niche (Pulliam 2000). While we provide the first insights into niche switching in a large partially migratory herbivore, it remains important to assess if differences in the realized niches between residents and migrants result in differences in demographic fitness to better understand the evolution of migratory plasticity (Lundberg 1988, Kaitala et al. 1993). For example, while migratory roe deer adjust their realized niche, it is uncertain if they are potentially pushed towards the edge of their fundamental niche space with decreased fitness or even sinks (Hirzel and Le Lay 2008). Overall, seasonal niches of migratory ungulates should be treated as dynamic entities over the annual cycle.

While we were unable to assess fitness consequences of migration, our analysis of the determinants for roe deer migration across five populations suggested that migration was a function of forage, terrain and climatic factors at the individual level. For example, average NDVI was highest for resident summer and winter niches, while the SD of NDVI was highest for migrant summer and winter niches. High NDVI for residents likely reflects higher coniferous canopy cover at lower elevations (Peters et al. in prep [Chapter 4]), because NDVI is highest in forests compared to open (meadow) areas (Gamon et al. 1995). Further, because variation in NDVI was higher for migrants, forage overall forage quality may be higher for migrants despite the higher overall NDVI of resident ranges. Similarly, contingency (seasonality) and overall predictability of NDVI was highest in migrant ranges. It has been shown that increased spatiotemporal variation in NDVI, regardless of open or closed canopies, is correlated with higher forage quality availability in the growing season (Hebblewhite et al. 2008). We also found that migratory roe deer used steeper slopes in both seasonal ranges, stayed in more rugged terrain and at higher elevations than resident roe deer during summer (Mysterud 1999, Cagnacci et al. 2011). We found winter severity to be a strong niche difference (Fig.3-6). Summer niches of migrants had the highest winter severity values, suggesting that migrants may need to escape from limiting winter conditions as suggested by other authors addressing roe deer migration (e.g. Mysterud et al. 1999, Cagnacci et al. 2011) or other ungulates (Nicholson et al. 1997, Ball et al. 2001). Cagancci et al. (2011) and (Peters et al. in prep [Chapter 4]) also found that roe deer migration increased in steep terrain with deeper snow cover.

It is commonly assumed that migratory and resident individuals from partially migratory populations reside in similar conditions when on sympatric ranges (Fryxell and Sinclair 1988, Hebblewhite and Merrill 2009, Jones et al. 2014). However, we found that winter niches of migrants and residents were different, although to a lesser degree than summer ranges. This suggests even if ranges of roe deer with different migratory behaviors may spatially overlap, or at least be in closer proximity in winter, individuals may show differences in fine-scale habitat selection behaviors (Senft et al. 1987). For example, Sanz-Auguilar et al. (2014) found that in migratory storks (*Ciconia ciconia*) there were more forage niche specialists among residents (72%) than migrants (40%) on their shared range, presumably because migrants may take advantage of different niches, because they are not as familiar with their habitat. Also, Zini (2015) found that resident roe deer used higher quality habitat than migratory roe deer in winter in one of our study areas (Italy – Val Rendena). Interestingly, Robinson et al. (2010) showed that elk with resident strategies were exposed to higher predation risk at night compared to animals with migratory strategies on their shared winter range in a partially migratory population, likely mediated by human activity. In contrast, we found that the nightlights index (Small et al. 2005), a suggested proxy for human activity and thus potentially harvest, was higher in migratory roe deer niches in winter compared to residents, although migrants had the lowest values in summer. Additionally, increased canopy closure was mainly associated with resident winter ranges, which indicates higher densities of protective cover against predators as well as thermoregulation benefits (Mysterud and Ostbye 1999). This indicates that migrants may have had higher vulnerability to human harvest and other sources of

mortality risk in winter, but not summer. While these results are concurrent with previous research that showed that migration decreases risk exposure for migrants (here, by leaving winter ranges; Fryxell and Sinclair 1988), our two risk indices should be viewed solely as suggestive of differences in risk exposure, especially in the absence of fitness comparisons. Overall, the result that sympatric migrant and resident roe deer do not share the same ecological niche even in winter has important implications for understanding the ecology and management of roe deer. For instance, if resident individuals are able to more effectively use winter ranges and avoid limiting conditions, e.g. by escaping risk factors or optimizing the use of feeding stations (Ossi 2014), we may expect changes in the relative benefits and costs of migration that may favor one strategy over another (Jones et al. 2014).

Which factor is more dominant in shaping and maintaining migratory behaviour at the individual level is likely an inverse function of density dependence (Fryxell and Sinclair 1998), which has been shown to affect migration probability with theoretical modelling and in empirical systems (Lundberg 1988). Partial migration is expected to be maintained in stochastic environments where density dependence is present (Lundberg 1988). For example, Eggeman et al. (*in review*) and Mysterud et al. (2011) showed that *Cervus spp*. migration increased with population density, consistent with the competition avoidance hypothesis. In our study, roe deer migration probability increased with increasing densities that depended on the level of spatial variation of seasonality in vegetation (Fig.3-7). We found that at low roe deer densities, migration probability for roe deer remained fairly low even when spatiotemporal variation of vegetation was high, but migration probability drastically

increased as both spatiotemporal variation of vegetation and density increased (Fig. 3-8). Thus, increased levels of spatial variation in seasonal vegetation, which was highest in the Italian study area in the Alps (Italy – Val Rendena; Fig.3-1), along with high densities favoured migration in roe deer in our roe deer populations.

Some characteristics of our study may have influenced our results. In this study we used a presence-only design to estimate niche differences. We did not compare environmental conditions at used sites with absence- or pseudo-absence data to define niche space availability. Broennimann et al. (2012) showed that when not correcting occurrence (use) by the environmental prevalence, niche overlap will be consistently underestimated except for niches with very low overlap. In our case, the availability for resident animals was consistent in both seasons and thus, our analysis will not affect their niche overlap. If niche overlap would be underestimated for migrants, our results would consequently only be stronger when correcting for availability. Thus, we feel that our results should be robust. Next, niche overlap can also only be detected accurately when variables driving species' distributions are known and those variables defining niches of migrants and residents may be measured at smaller scales (Hirzel and Le Lay 2008). For example, while our results support niche switching for migratory roe deer, habitat selection processes are generally scale-dependent (Senft et al. 1987, Wiens 1989, Johnson et al. 2001). Although we found no niche following as a function of fairly high resolution environmental covariates, niche following could occur at smaller spatial scales, such as forage selection. However, this may be expected more for grazers with narrower feeding niches. Roe deer are concentrate selectors, with a very broad feeding niche and high seasonal

plasticity in forage species intake (Redjadj et al. 2014). Thus, we assume that niche following is unlikely for both residents and migrants at smaller scales, but rather suggest that migratory roe deer may take advantage of improved forage (Peters et al. in prep [Chapter 2]) and escape density-dependence in summer through niche switching. Also, future research should expand to other partially migratory ungulates with different migration patterns. For example, Sierra Nevada bighorn sheep (*Ovis Canadensis sierra*) are partially migratory, where residents maintain year-round alpine ranges and migrants spend the winter at lower elevations. While resident individuals endure extreme winter conditions, migratory bighorn sheep are believed to be significantly impacted by apparent competition with neighboring mule deer herds that support increased populations of mountain lions (*Puma concolor*) through apparent competition). Biotic factors (density-dependence or predation) may drive partially migratory individuals to switch seasonal niches.

In conclusion, the niche concept provides a strong framework for framing questions surrounding the patterns and the determinants underlying migration (Jonzén et al. 2011). Future changes including climate change and anthropogenic landscape alteration will affect the niches of migrants, residents and other movement behaviors in between these two endpoints of the continuum. Understanding the functional importance of key components of spatiotemporal niche variability will offer insights into linking predicted future resource dynamics to movement behaviors.

LITERATURE CITED

Albon, S. D. and R. Langvatn. 1992. Plany Phenology and the Benefits of Migration in a Temperate Ungulate. Oikos **65**:502-513.

Arnold, T. W. 2010. Uninformative Parameters and Model Selection Using Akaike's Information Criterion. Journal of Wildlife Management **74**:1175-1178.

Ball, J. P., C. Nordengren, and K. Wallin. 2001. Partial migration by large ungulates: characteristics of seasonal moose *Alces alces* ranges in northern Sweden. Wildlife Biology **7**:39-47.

Bischof, R., L. E. Loe, E. L. Meisingset, B. Zimmermann, B. Van Moorter, and A. Mysterud. 2012. A Migratory Northern Ungulate in the Pursuit of Spring: Jumping or Surfing the Green Wave? American Naturalist **180**:407-424.

Broennimann, O., M. C. Fitzpatrick, P. B. Pearman, B. Petitpierre, L. Pellissier, N. G. Yoccoz, W. Thuiller, M.-J. Fortin, C. Randin, N. E. Zimmermann, C. H. Graham, and A. Guisan. 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. Global Ecology and Biogeography **21**:481-497.

Bunnefeld, N., L. Börger, B. van Moorter, C. M. Rolandsen, H. Dettki, E. J. Solberg, and G. Ericsson. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. Journal of Animal Ecology **80**:466-476.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, USA.

Burnham, K. P. and D. R. Anderson. 2004. Multimodel inference - understanding AIC and BIC in model selection. Sociological Methods & Research **33**:261-304.

Börger, L. and L. M. Fryxell. 2012. Quantifying individual differences in dispersal using net squared displacement.*in* J. Clobert, M. Baguette, T. Benton, and J. Bullock, editors. Dispersal and spatial evolutionary ecology. Oxford Univer-sity Press, Oxford, UK.

Cagnacci, F., S. Focardi, A. Ghisla, B. Van Moorter, E. Gurarie, M. Heurich, A. Mysterud, J. Linnell, M. Panzacchi, and M. Roel. in revision. How many routes lead to migration? Re-establishing the link between definitions, methods and movemet ecology. Journal of Animal Ecology.

Cagnacci, F., S. Focardi, M. Heurich, A. Stache, A. J. M. Hewison, N. Morellet, P. Kjellander, J. D. C. Linnell, A. Mysterud, M. Neteler, L. Delucchi, F. Ossi, and F. Urbano. 2011. Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. Oikos **120**:1790-1802.

Chapman, B. B., K. Hulthen, D. R. Blomqvist, L. A. Hansson, J. A. Nilsson, J. Brodersen, P. A. Nilsson, C. Skov, and C. Bronmark. 2011. To boldly go: individual differences in boldness influence migratory tendency. Ecology Letters **14**:871-876.

Chessel, D., A. B. Dufour, and J. Thioulouse. 2004. The ade4 package-I- One-table methods. R News. 4: 5-10.

Colwell, R. K. 1974. Predictability, Constancy, and Contingency of Periodic Phenomena. Ecology **55**:1148-1153.

Dingle, H. and V. A. Drake. 2007. What is migration? Bioscience **57**:113-121.

Doledec, S. and D. Chessel. 1987. Rythmes saisonniers et composantes stationnelles en milieu aquatique. I. Description d'un plan d'observations complet par projection de variables. Acta Oecologica, Oecologia Generalis **8**:403-426.

English, A. K., A. L. Chauvenet, K. Safi, and N. Pettorelli. 2012. Reassessing the determinants of breeding synchrony in ungulates. PloS one **7**:e41444.
Fieberg, J. and C. O. Kochanny. 2005. Quantifying home-range overlap: The importance of the utilization distribution. Journal of Wildlife Management **69**:1346-1359.
Franklin, J. 2010. Mapping Species Distributions: Spatial Inference and Prediction. Cambridge University Press, Cambridge.
Fryxell, J. M. and A. R. E. Sinclair. 1988. Causes and Consequences of Migration by Large Herbivores. Trends in Ecology & Evolution **3**:237-241.
Fryxell, J. M., J. F. Wilmshurst, and A. R. E. Sinclair. 2004. Predictive models of movement by Serengeti grazers. Ecology **85**:2429-2435.
Gaidet, N. and P. Lecomte. 2013. Benefits of migration in a partially-migratory tropical ungulate. BMC Ecology **13**.
Gamon, J. A., C. B. Field, M. L. Goulden, K. L. Griffin, A. E. Hartley, G. Joel, J. Penuelas, and R. Valentini. 1995. Relationships Between NDVI, Canopy Structure, and Photosynthesis in Three Californian Vegetation Types. Ecological Society of America.
Gillies, C., M. Hebblewhite, S. E. Nielsen, M. Krawchuk, C. Aldridge, J. Frair, C. Stevens, D. J. Saher, and C. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology **75**:887-898.
Gordon, I. J., A. J. Hester, and M. Festa-Bianchet. 2004. REVIEW: The management of wild large herbivores to meet economic, conservation and environmental objectives. Journal of Applied Ecology **41**:1021-1031.
Gower, J. C. 1971. A general coefficient of similarity and some of its properties. Biometrics **27**:857-874.
Grosbois, V., O. Gimenez, J. M. Gaillard, R. Pradel, C. Barbraud, J. Clobert, A. P. Møller, and H. Weimerskirch. 2008. Assessing the impact of climate variation on survival in vertebrate populations. Biological Reviews **83**:357-399.
Hansen, M. C., P. V. Potapov, R. Moore, M. Hancher, S. A. Turubanova, A. Tyukavina, D. Thau, S. V. Stehman, S. J. Goetz, T. R. Loveland, A. Kommareddy, A. Egorov, L. Chini, C. O. Justice, and J. R. G. Townshend. 2013. High-Resolution Global Maps of 21st-Century Forest Cover Change. Science **342**:850-853.
Hebblewhite, M., E. Merrill, and G. McDermid. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. Ecological Monographs **78**:141-166.
Hebblewhite, M. and E. H. Merrill. 2009. Trade-offs between wolf predation risk and forage at multiple spatial scales in a partially migratory ungulate. Ecology **26**:54-59.
Hein, A. M., C. Hou, and J. F. Gillooly. 2012. Energetic and biomechanical constraints on animal migration distance. Ecology Letters **15**:105-110.
Hewison, A. J. M., J.-P. Vincent, and D. Reby. 1998. Social organisation of European roe deer.
Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology **25**:1965-1978.
Hirzel, A. H. and G. Le Lay. 2008. Habitat suitability modelling and niche theory. Journal of Applied Ecology **45**:1372-1381.

Hobbs, N. T. 1996. Modification of Ecosystems by Ungulates. The Journal of Wildlife Management **60**:695-713.

Hopcraft, J. G. C., J. Morales, H. Beyer, M. Borner, E. Mwangomo, A. Sinclair, H. Olff, and D. T. Haydon. 2014. Competition, predation, and migration: individual choice patterns of Serengeti migrants captured by hierarchical models. Ecological Monographs **84**:355-372.

Hosmer, D. W. and S. Lemeshow, editors. 2000. Applied Logistic Regression. John Wiley and Sons, New York, USA.

Hutchinson, G. E. 1957. Concluding remarks. Pages 415-427 *in* Cold Spring Harbour Symposium on Quantitative Biology

Johnson, C. J., K. L. Parker, and D. C. Heard. 2001. Foraging across a variable landscape: behavioral decisions made by woodland caribou at multiple spatial scales. Oecologia **127**:590-602.

Jones, J. D., M. J. Kauffman, K. L. Monteith, B. M. Scurlock, S. E. Albeke, and P. C. Cross. 2014. Supplemental feeding alters migration of a temperate ungulate. Ecological Applications **24**:1769-1779.

Jongman, R. H. G., C. J. F. Ter Braak, and O. F. R. Van Tongeren. 1995. Data analysis in community and landscape ecology. Cambridge University Press.

Jonzén, N., E. Knudsen, R. D. Holt, and B. E. Sæther. 2011. Uncertainty and predictability: the niches of migrants and nomads. Pages 91-109 *in* E. J. Milner-Gulland, J. M. Fryxell, and A. R. E. Sinclair, editors. Animal migration: A synthesis. Oxford University Press, Oxford.

Kaitala, A., V. Kaitala, and P. Lundberg. 1993. A Theory of Partial Migration. American Naturalist **142**:59-81.

Laube, I., C. H. Graham, and K. Böhning-Gaese. 2015. Niche availability in space and time: migration in Sylvia warblers. Journal of Biogeography:n/a-n/a.

LeResche, R. E. 1974. Moose migrations in North America. Naturaliste Canadien **101**:393-415.

Linnell, J. D. C., P. Duncan, and R. Andersen. 1998. The European roe deer: A portrait of a successfulk species.*in* R. Andersen, P. Duncan, and J. D. C. Linnell, editors. The European roe deer: the biology of success. Scandinavian University Press, Oslo.

Lone, K., L. E. Loe, T. Gobakken, J. D. C. Linnell, J. Odden, J. Remmen, and A. Mysterud. 2014. Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. Oikos **123**:641-651.

Lundberg, P. 1988. The Evolution of Partial Migration in Birds. Trends in Ecology & Evolution **3**:172-175.

Maechler, M., P. Rousseeuw, A. Struyf, M. Hubert, and K. Hornik. 2015. cluster: Cluster Analysis Basics and Extensions. R package version 2.0.1.

Maselli, F. 2004. Monitoring forest conditions in a protected Mediterranean coastal area by the analysis of multiyear NDVI data. Remote Sensing of Environment **89**:423-433.

McClintock, B. T., R. King, L. Thomas, J. Matthiopoulos, B. J. McConnell, and J. M. Morales. 2012. A general discrete-time modeling framework for animal movement using multistate random walks. Ecological Monographs **82**:335-349.

Melis, C., B. Jędrzejewska, M. Apollonio, K. A. Bartoń, W. Jędrzejewski, J. D. C. Linnell, I. Kojola, J. Kusak, M. Adamic, S. Ciuti, I. Delehan, I. Dykyy, K. Krapinec, L. Mattioli, A. Sagaydak, N. Samchuk, K. Schmidt, M. Shkvyrya, V. E. Sidorovich, B. Zawadzka, and S. Zhyla. 2009. Predation has a greater impact in less productive environments: variation in roe deer, Capreolus capreolus, population density across Europe. Global Ecology and Biogeography **18**:724-734.

Middleton, A. D., M. J. Kauffman, D. E. McWhirter, J. G. Cook, R. C. Cook, A. A. Nelson, M. D. Jimenez, and R. W. Klaver. 2013. Animal migration amid shifting patterns of phenology and predation: Lessons from a Yellowstone elk herd. Ecology.

Morellet, N., C. Bonenfant, L. Börger, F. Ossi, F. Cagnacci, M. Heurich, P. Kjellander, J. D. C. Linnell, S. Nicoloso, P. Sustr, F. Urbano, and A. Mysterud. 2013. Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. Journal of Animal Ecology **82**:1326-1339.

Mueller, T., K. A. Olson, G. Dressler, P. Leimgruber, T. K. Fuller, C. Nicolson, A. J. Novaro, M. J. Bolgeri, D. Wattles, S. DeStefano, J. M. Calabrese, and W. F. Fagan. 2011a. How landscape dynamics link individual- to population-level movement patterns: a multispecies comparison of ungulate relocation data. Global Ecology and Biogeography **20**:683-694.

Mysterud, A. 1999. Seasonal migration pattern and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway. Journal of Zoology **247**:479-486.

Mysterud, A., R. Bischof, L. E. Loe, J. Odden, and J. Linnell. 2012. Contrasting migration tendencies of sympatric red deer and roe deer suggest multiple causes of migration in ungulates. Ecosphere 3:10, art92.

Mysterud, A., D. O. Hessen, R. Mobaek, V. Martinsen, J. Mulder, and G. Austrheim. 2011a. Plant quality, seasonality and sheep grazing in an alpine ecosystem. Basic and Applied Ecology **12**:195-206.

Mysterud, A., L. E. Loe, B. Zimmermann, R. Bischof, V. Veiberg, and E. Meisingset. 2011b. Partial migration in expanding red deer populations at northern latitudes - a role for density dependence? Oikos **120**:1817-1825.

Mysterud, A. and E. Ostbye. 1995. Bed-site selection by European roe deer (Capreolus capreolus) in southern Norway during winter. Canadian Journal of Zoology-Revue Canadienne De Zoologie **73**:924-932.

Mysterud, A. and E. Ostbye. 1999. Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. Wildlife Society Bulletin **27**:385-394.

Naidoo, R., P. Du Preez, G. Stuart-Hill, M. Jago, and M. Wegmann. 2012. Home on the Range: Factors Explaining Partial Migration of African Buffalo in a Tropical Environment. Plos One **7**:e36527.

Nakazawa, Y., A. T. Peterson, E. Martínez-Meyer, and A. G. Navarro-Sigüenza. 2004. Seasonal Niches of Nearctic-Neotropical Migratory Birds: Implications for the Evolution of Migration. The Auk **121**:610-618.

Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement

research. Proceedings of the National Academy of Sciences of the United States of America **105**:19052-19059.
Nelson, M. E. 1995. Winter range arrival and departure of white-tailed deer in northeastern Minnesota. Canadian Journal of Zoology **73**:1069-1076.
Nicholson, M. C., R. T. Bowyer, and J. G. Kie. 1997. Habitat selection and survival of mule deer: Tradeoffs associated with migration. Journal of Mammalogy **78**:483-504.
Ossi, F. 2014. Ecological determinants of roe deer (Capreolus capreolus) spatial behavior and movement in limiting conditions. Université Claude Bernard – Lyon 1, Lyon, France.
Peterson, M. N., R. R. Lopez, P. A. Frank, M. J. Peterson, and N. J. Silvy. 2003. Evaluating capture methods for urban white-tailed deer. Wildlife Society Bulletin **31**:1176-1187.
Pulliam, H. R. 2000. On the relationship between niche and distribution. Ecology Letters **3**:349-361.
R Development Core Team. 2013. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. .
Ramanzin, M., E. Sturaro, and D. Zanon. 2007. Seasonal migration and home range of roe deer (Capreolus capreolus) in the Italian eastern Alps. Canadian Journal of Zoology-Revue Canadienne De Zoologie **85**:280-289.
Redjadj, C., G. Darmon, D. Maillard, T. Chevrier, D. Bastianelli, H. Verheyden, A. Loison, and S. Saïd. 2014. Intra- and Interspecific Differences in Diet Quality and Composition in a Large Herbivore Community. PloS one **9**:e84756.
Rousseeuw, P. J. 1987. Silhouettes: A graphical aid to the interpretation and validation of cluster analysis. Journal of Computational and Applied Mathematics **20**:53-65.
Sabine, D. L., S. F. Morrison, H. A. Whitlaw, W. B. Ballard, G. J. Forbes, and J. Bowman. 2002. Migration behavior of white-tailed deer under varying winter climate regimes in New Brunswick. Journal of Wildlife Management **66**:718-728.
Sanz-Aguilar, A., R. Jovani, C. J. Melián, R. Pradel, and J. L. Tella. 2014. Multi-event capture–recapture analysis reveals individual foraging specialization in a generalist species. Ecology **96**:1650-1660.
Schoener, T. W. 1974. Resource partitioning in ecological communities. Science **185**:27-39.
Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. Bioscience **37**:789-795 & 798-799.
Sih, A., J. Cote, M. Evans, S. Fogarty, and J. Pruitt. 2012. Ecological implications of behavioural syndromes. Ecology Letters **15**:278-289.
Singh, N. J., L. Borger, H. Dettki, N. Bunnefeld, and G. Ercsson. 2012. From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. Ecological Applications **22**:2007-2020.
Skov, C., H. Baktoft, J. Brodersen, C. Bronmark, B. Chapman, L. A. Hansson, and P. A. Nilsson. 2011. Sizing up your enemy: individual predation vulnerability predicts migratory probability. Proceedings of the Royal Society B-Biological Sciences **278**:1414-1418.

Small, C., F. Pozzi, and C. D. Elvidge. 2005. Spatial analysis of global urban extent from DMSP-OLS night lights. Remote Sensing of Environment **96**:277-291.
Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. Ecology Letters **10**:1115-1123.
Soberón, J. and M. Nakamura. 2009. Niches and distributional areas: Concepts, methods, and assumptions. Proceedings of the National Academy of Sciences **106**:19644-19650.
Southwood, T. R. E. 1962. Migration of terrestrial arthropods in relation to habitat. Biological Reviews **37**:171-211.
Taylor, C. M. and D. R. Norris. 2007. Predicting conditions for migration: effects of density dependence and habitat quality. Biology Letters **3**:280-283.
Teitelbaum, C. S., W. F. Fagan, C. H. Fleming, G. Dressler, J. M. Calabrese, P. Leimgruber, and T. Mueller. 2015. How far to go? Determinants of migration distance in land mammals. Ecology Letters **18**:545-552.
ter Braak, C., editor. 1992. Permutation versus bootstrap significance tests in multiple regression and ANOVA. Springer-Verlag, Berlin, Germany.
ter Braak, C. 1995. Chapter 5: Ordination. Pages 91-173 *in* R. Jongman, C. ter Braak, and O. Van Tongeren, editors. Data analysis in community and landscape ecology. Cambridge University Press, Cambridge, UK.
Turchin, P. 1998. Quantitative Analysis of Movement: measuring and modeling population redistribution in plants and animals. Sinauer Associates Sunderland, MA.
Wahlström, L. K. and O. Liberg. 1995. Patterns of dispersal and seasonal migration in roe deer (Capreolus capreolus). Journal of Zoology **235**:455-467.
Wiens, J. A. 1989. Spatial Scaling in Ecology. Functional Ecology **3**:385-397.
Zini, V. 2015. Tattiche di movimento contrastanti e differenze nell'utilizzo dell'habitat del capriolo (Capreolus capreolus) a livello stagionale in ambiente alpino. Univerity of Rome - La Sapienza, Rome.

Table 3-1. Proportions of roe deer (*Capreolus capreolus*) classified into seasonal movement behaviors across five populations in Europe based the geographic distance, ecological distance, spatial clustering, and integrated approach using a k-means clustering algorithm. The integrated approach identified two clusters, where cluster 1 was characterized by roe deer showing predominantly resident characteristics, while cluster 2 was characterized by animals showing predominantly characteristics of migrant animals. Roe deer GPS data were collected between 2005 and 2013.

Population[1]	**DE/CZ**	**IT.2**	**IT.1**	**NO**	**SE**
		Geographical distance (NSD)			
Residents	0.35	0.14	0.18	0.08	0.29
Mixed Migrants	0.42	0.43	0.27	0.46	0.64
Dispersers	0.08	0.14	0.27	0.08	0.07
Migrants	0.15	0.29	0.27	0.38	0.00
		Ecological distance (ED)			
Residents	0.38	0.14	0.27	0.07	0.23
Mixed Migrants	0.50	0.29	0.55	0.64	0.46
Dispersers	0.04	0.14	0.00	0.29	0.00
Migrants	0.08	0.43	0.18	0.00	0.31
		Spatial Clustering			
Residents	0.65	0.29	0.27	0.46	0.86
Migrants	0.35	0.71	0.73	0.54	0.14
		Integrated Approach			
Cluster 1	0.81	0.57	0.45	0.69	1

Table 3.1. continued

Cluster 2	0.19	0.43	0.55	0.31	0

[1] DE/CZ = Germany/Czech Republic (N=26), IT.2= Italy-Monte Bondone (N=11), SE= Sweden (N=14), NO = Norway (N=13), IT.1=Italy-Val Rendena (N=7)

Table 3-2. Averages and standard deviations (SD; in parenthesis) for different roe deer (*Capreolus capreolus*) migration measures identified by k-means cluster analysis with k=2 (C_R = resident cluster, C_M = migrant cluster). Migration measures include the difference in ecological distance between winter 1versus summer ($ED_{wi1\text{-}su}$), the annual SD, the asymptote from ED models, the Schoener's niche overlap (D) between winter and the following summer, the % of individuals classified as migrants based on the seasonal clustering method, the associated distance between cluster centers, and the asymptote of the NSD. Finally, the Silhouette widths are provided for each cluster.

	C_R	**C_M**
Ecological Distance		
$ED_{wi\text{-}su}$	1.72 (0.980)	4.48 (1.593)
SD	0.68 (0.349)	1.91 (0.806)
Asymptote ED*	0.002 (0.001)	0.01 (0.002)
Seasonal Niche Overlap		
Schoener's D	0.61 (0.200)	0.22 (0.175)
Seasonal location overlap		
% migration	25	100
Cluster Distance (km)	1.47 (2.822)	10.68 (8.202)
Cartesian Distance		
Asymptote NSD*[1] (km)	1.54 (4.165)	10.59 (8.247)
K-means Clustering		
Silhouette width	0.55 (0.190)	0.48 (0.152)

*square root transformed and multiplied by 10 00 00, *[1]square root transformed

Table 3-3. Means of variables and results of the linear discriminant analysis using averaged environmental data by season (winter and summer) and individual roe deer (*Capreolus capreolus*) of each cluster separating migrant clusters (C_M) and resident clusters (C_R) as input matrix. Canonical scores (CS) represent the standardized canonical discriminant function coefficients of all variables along the two dimensions identified. The class scores (DS) represent the centroid coefficients of each group (group centroids) in ordination space defined by the two dimensions.

	Covariate means by group				**Canonical Scores**	
Covariates	**C_R Su**	**C_M Su**	**C_R Wi**	**C_M Wi**	**CS1**	**CS2**
Canopy closure	47.07	38.25	51.94	46.67	0.17	0.24
Nightlights	11.15	5.08	12.74	20.16	-0.08	0.35
Constancy	0.25	0.21	0.28	0.28	0.10	0.41
Contingency	0.32	0.39	0.30	0.33	-0.27	-0.38
Elevation (m)	575.62	1232.38	566.54	825.03	-0.55	-0.44
Slope (degrees)	9.22	12.64	9.71	19.39	-0.48	0.21
Predictability	0.58	0.60	0.58	0.61	-0.28	0.02
% Human lc	1.49	0.00	3.64	3.49	0.01	0.17
% Agricultue lc	20.51	29.09	8.80	5.28	0.03	-0.41
% Deciduous lc	11.94	4.97	5.62	16.34	-0.06	0.14
% Wetland lc	0.84	4.38	0.03	0.17	-0.16	-0.37
% Conifer lc	2.49	2.51	1.48	11.56	-0.24	-0.37
% Mixed lc	37.06	24.97	48.12	37.04	0.15	0.21
% Shrubs lc	25.67	34.07	32.30	26.12	-0.02	-0.06

Table 3-3. continued

Winter severity	0.59	0.73	0.58	0.50	-0.03	-0.51
Ruggedness	10.88	12.83	11.25	22.78	-0.40	0.26
Annual average temp.	6.50	5.69	6.06	6.88	-0.08	0.17
NDVI SD	0.11	0.18	0.11	0.18	-0.80	-0.12
NDVI average	0.76	0.71	0.76	0.71	0.52	0.09
DS1	0.51	-1.04	0.31	-1.43	---	---
DS2	-0.12	-1.50	0.24	1.06	---	---

Table 3-4. Candidate logistic regression models describing the probability of migration for roe deer (*Capreolus capreolus*) in five Europen study areas. Predictor variables included population density, the overall predictability (predictability) of the Normalized Difference Vegetation Index (NDVI; a measure of vegetation productivity), between-year variability of NDVI (constancy) and seasonality of NDVI (contingency). The SD of these three measures gives an index of spatiotemporal variation of NDVI measured within annual ranges of roe deer. The R^2_{ANODEV} describes the proportion of variation in migration probability that is accounted for by any given variable describing temporal or their spatiotemporal variation. We provide the model coefficients (β) for density and the additional parameters included in each model (x), their p-values (p), Akaike Information Criterion for small sample sizes (AICc), the difference in AICc to the null model (ΔAICc to M_i) and the R^2_{ANODEV}. GPS movement data were collected between 2005 and 2013.

Model	$\beta_{density}$	β_x	$p_{density}$	p_x	**AICc**	**ΔAICc to M_i**	R^2_{ANODEV}
M_i (intercept model)					82.40	0.00	
M_1 (M_i + density)	1.673		0.004		73.94	-8.46	1.00
M_1 + predictability	1.559	6.500	0.009	0.371	75.44	-6.95	0.05
M_1 + constancy	1.617	-4.991	0.006	0.171	73.86	-8.54	0.17
M_1 + contingency	1.456	7.162	0.014	0.078	72.53	-9.87	0.25
M_1 + predictability sd*	2.289	1.160	0.002	0.005	65.76	-16.64	0.49
M_1 + constancy sd*	1.690	1.083	0.005	0.005	65.58	-16.82	0.50
M_1 + contingency sd*	1.687	2.993	0.016	0.002	63.20	-19.20	0.55

* Log transformed

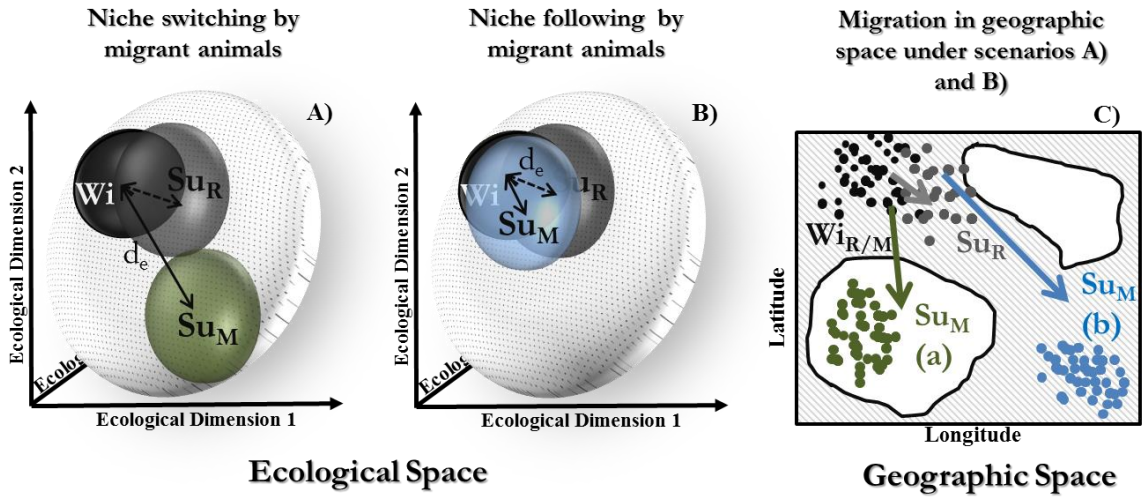


Figure 3-1. Conceptual representation of the hypothesized relationship between the ecological distance (d_e) and seasonal niche overlap under two hypotheses; A) seasonal niche switching by migrant animals and B) seasonal niche following by migrant animals. Residents are assumed to be conservative in their seasonal niches (always follow their seasonal niches). The dotted area in panels A) and B) represents the *fundamental niche* of the species and the colored areas represent the *realized seasonal* niches, where migrants that switch niches are displayed in green, migrants that follow niches are displayed in blue and resident summer niches are grey. Shared winter niches of both residents and migrants are displayed in black. Panel C) shows the distribution of the realized seasonal niches in geographic space, where residents maintain winter and summer ranges with high spatial overlap in close proximity. While migrants always move Cartesian distances between summer and winter ranges, they may switch to different habitats (a; niche switching) or move to similar habitats (b; niche following).

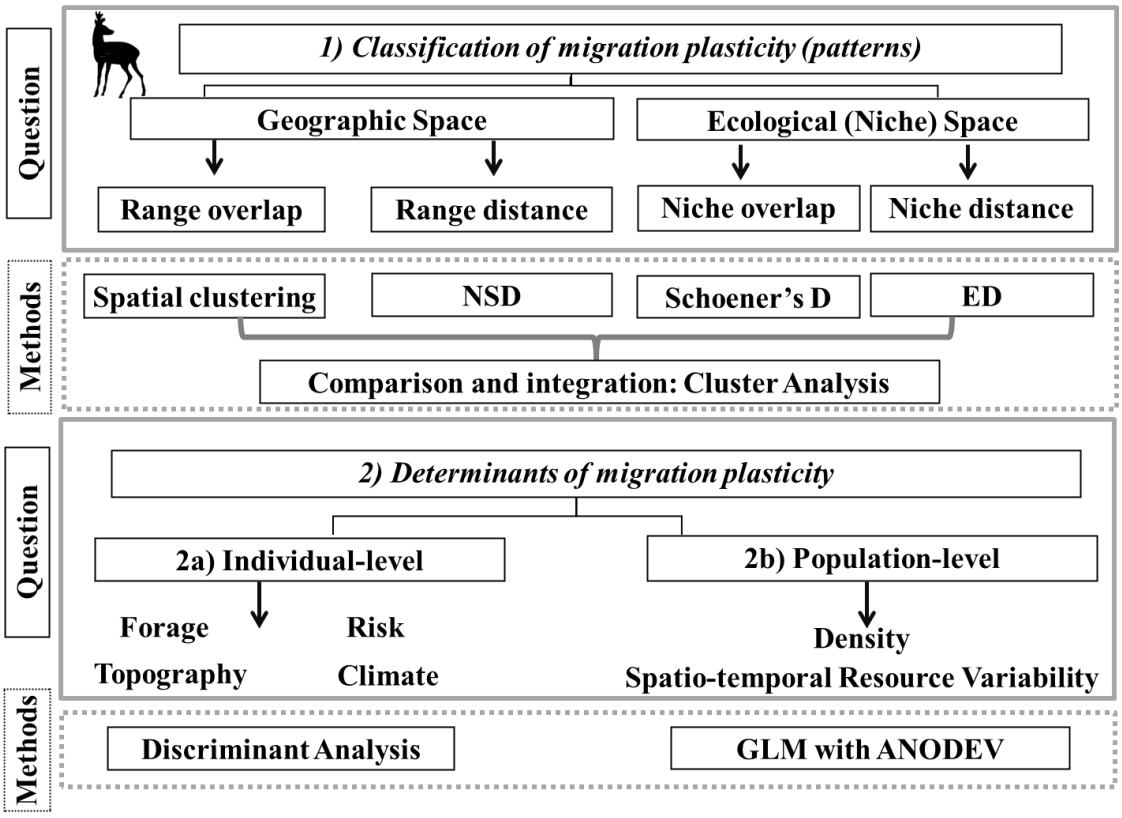


Figure 3-2. Conceptual Figure of workflow to study plasticity in migration behavior in a small ungulate, the European roe deer (*Capreolus capreolus*), across five European study areas using GPS movement data collected between 2005 and 2013. Each set of questions is followed by the methods used to address them.

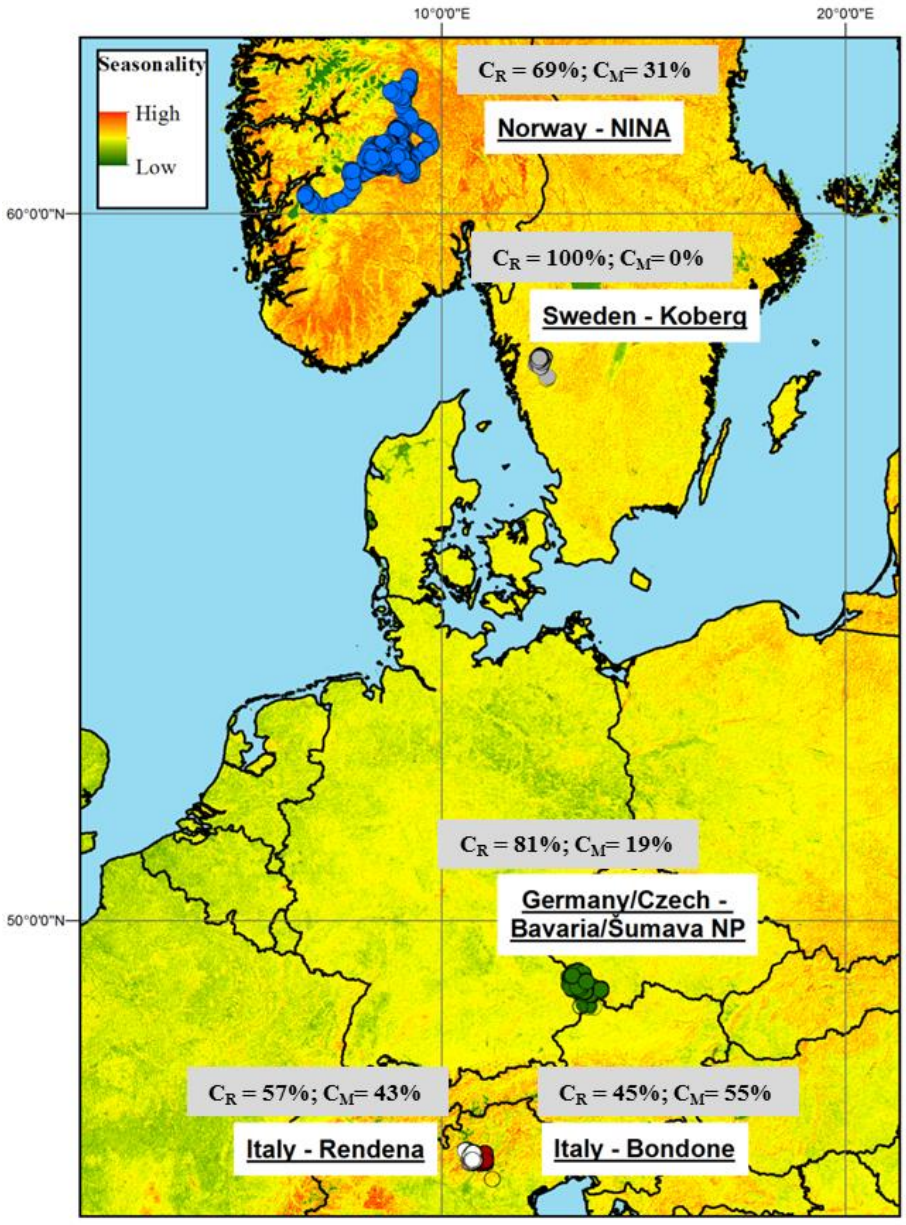


Figure 3-3. Global Positioning System (GPS) collar data of 71 roe deer (*Capreolus capreolus*) that were collected between 2005 and 2013 in five European study areas. The grey boxes give the percentages of individual roe deer classified as either residents (C_R) or migrants (C_M) using our integrated classification approach. The background shows seasonality of vegetation measured as contingency (Colwell 1974) of the Normalized Difference Vegetation Index across a time series from 2000 to 2014.

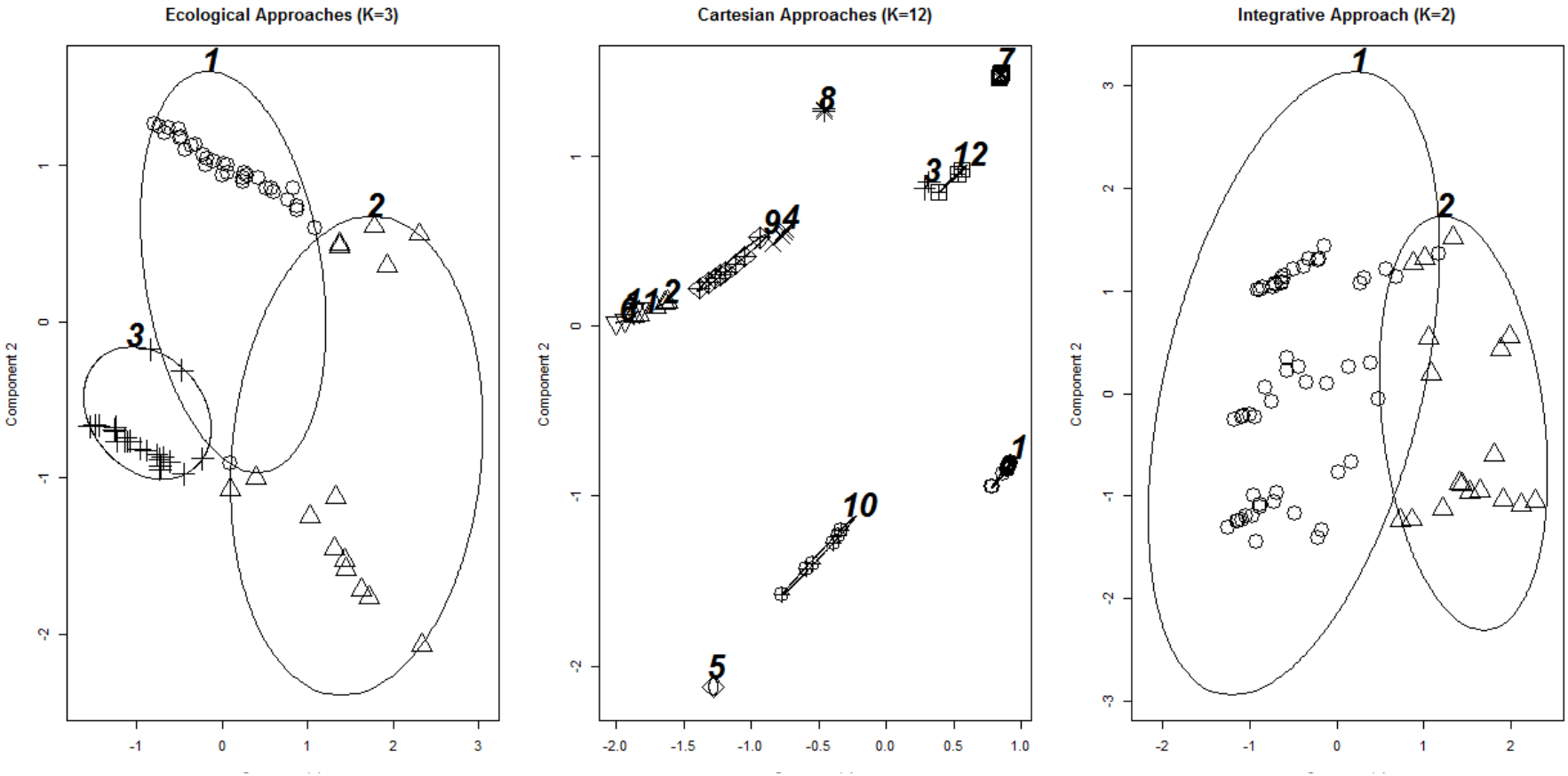


Figure 3- 4. Clusters identified based on the highest average Silhouette width for ecological distance approaches only ($\bar{s}$(k) = 0.45; left panel), Cartesian approaches only ($\bar{s}$(k) =0.86; center panel) and the integrative classification with the ecological and Cartesian approaches combined ($\bar{s}$(k) = 0.51; right panel).

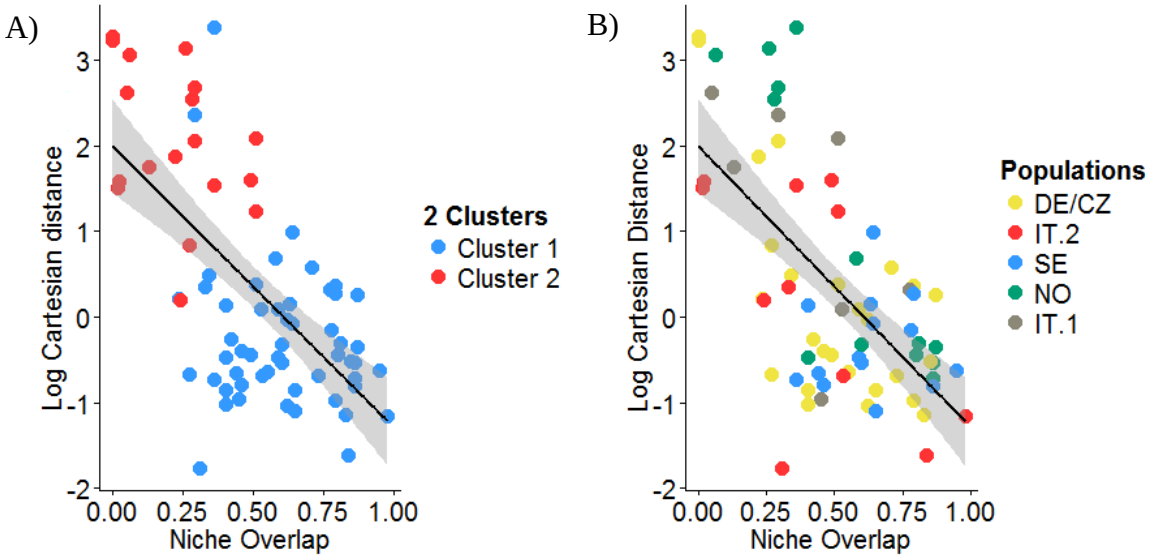


Figure 3-5. Schoener's niche overlap (D) against the log-transformed Cartesian migration distance (with 95%CI) by A) the classification using the integrated k-means cluster analysis into resident (Cluster 1; N=53) and migrant (Cluster 2; N=18) roe deer (*Capreolus capreolus*). Panel B) shows the same relationship by study populations used including Germany/Check Republic (DE/CZ, N=26), Italy-Monte Bondone (IT.2, N=11), Sweden (SE, N=14), Norway (NO, N=13) and Italy-Val Rendena (IT.1, N=7).

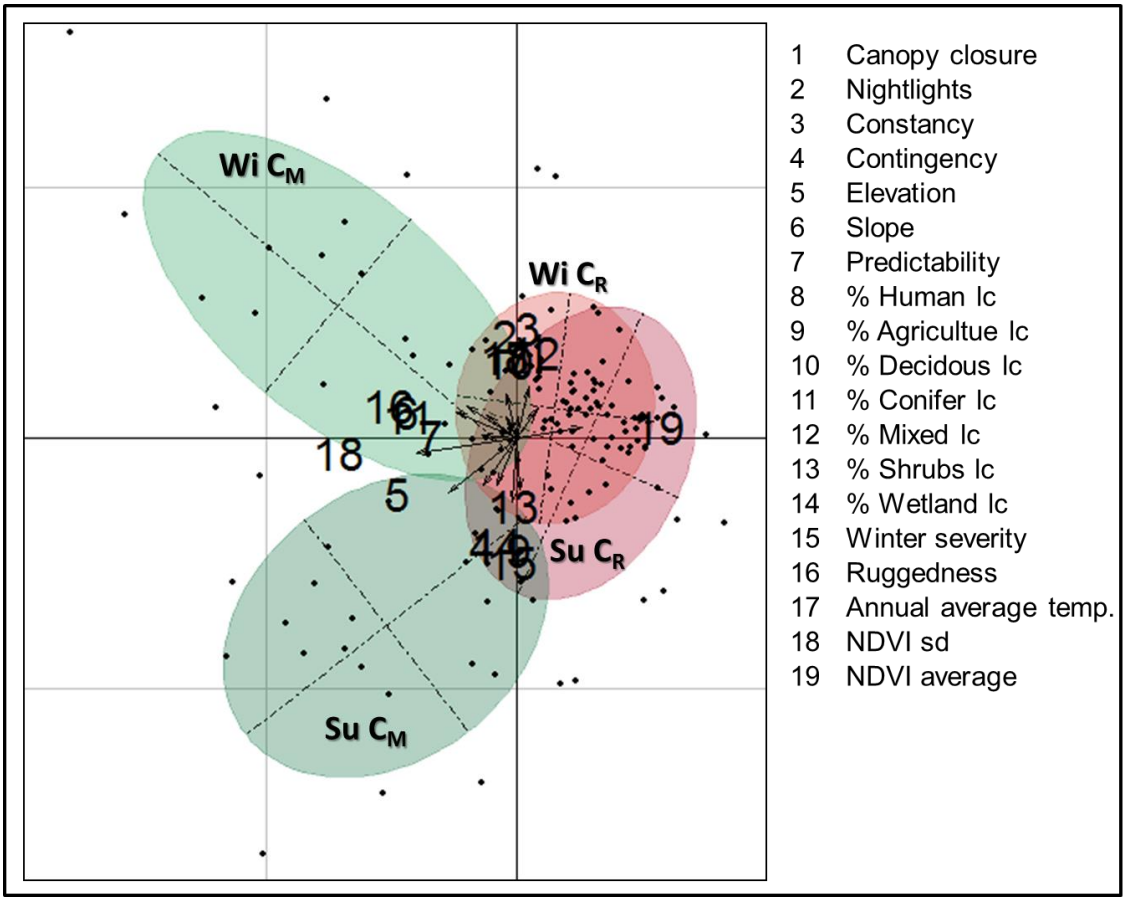


Figure 3-6. Canonical plot of the first two canonical axes of the discriminant analysis on environmental variables averaged for GPS location data of roe deer (*Capreolus capreolus*) classified into two groups (migrant cluster (C_M, green; N=18) and resident cluster (C_R, red; N=53) and two seasons (summer and winter). The plot shows the canonical scores (i.e. coefficients) of the linear discriminant function on the first two axes of the analysis. Overlaid are the projections of individual observations averaged for each animal by season (black points) and groups are displayed as colored ellipses, where the centers represent the group means (the between variances) and the ellipses are the within group variances. Roe deer GPS location data were collected between 2005 and 2013 in five European study areas.

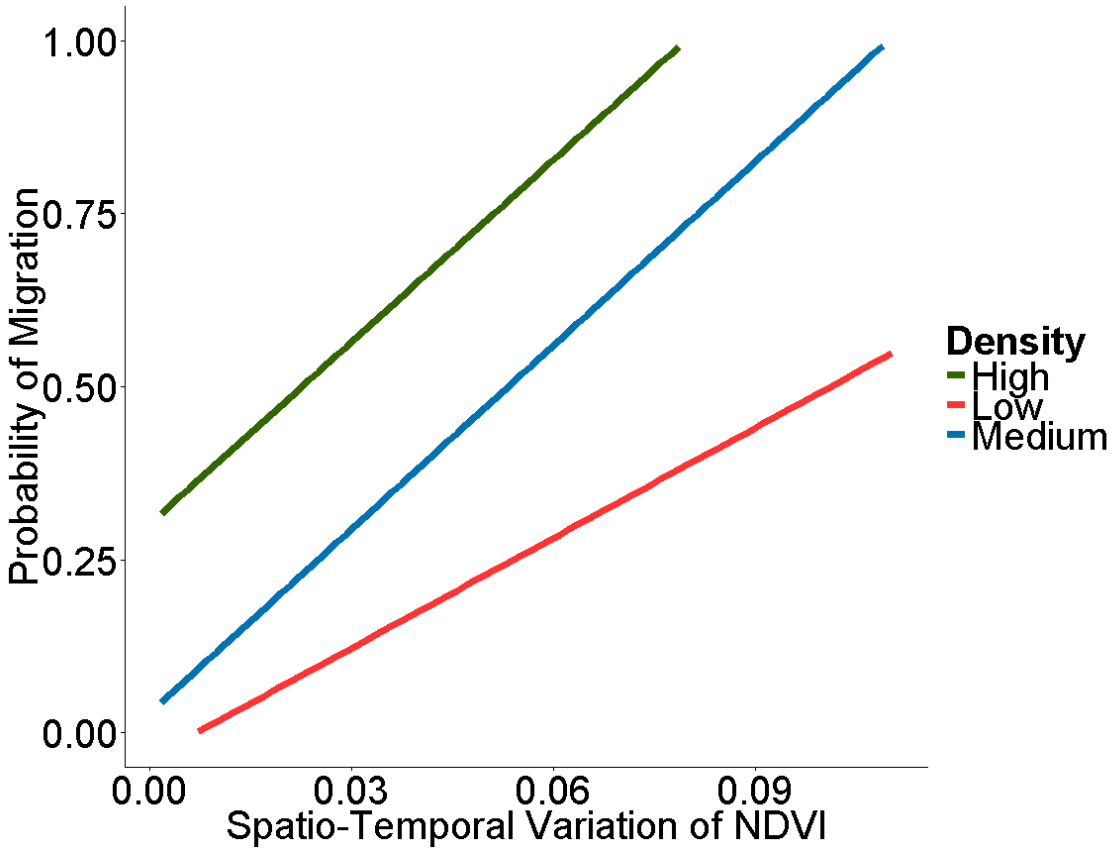


Figure 3-7. Model predictions from our top logistic regression model explaining migration probability in roe deer (*Caproelus capreolus*) as a function of spatial variation of seasonal vegetation resources (SD of contingency measured within annual roe deer ranges) given three levels of population density (high, medium and low) across five European study populations. Contingency was estimated with time series data of the Normalized Difference Vegetation Index (NDVI) collected between 2000 and 2014. Roe deer were monitored between 2005 and 2013.

APPENDIX 3-A. General characteristics of the five study areas from which we used roe deer (*Capreolus capreolus*) GPS data collected between 2005 and 2013. We used the following sample sizes: N=7, IT.1; N=11, IT.2; N=26, DE/CZ; N=14, SE; N=13, NO. Population densities were estimated for the same years as GPS data were collected. We list the density estimation methods used and the reclassified density index used in this study ranging from 1 to 3, where 1 means low, 2 means medium and 3 means high density.

Population	**Average lat/long**	**Habitat caracteristics**	**Elevation (m)**	**Institution**	**Density estimates (N/km^2)**
Italy – Bondone (IT.2)	46.0429 N, 11.0429E	alpine mountain range	400-1600	Edmund Mach Foundation	3.3. – 9.4, fecal pellet distance sampling, density class = 3
Italy – Rendena (IT.1)	46.0883 N, 11.7379E	alpine mountain range	490-2210	Edmund Mach Foundation	1.35- 2.53, fecal pellet distance sampling, density class = 2
Germany/ Czech republic - Bavaria (DE/CZ)	49.970 N, 13.3794E	central European sub-mountainous forest	650-1450	Bavarian Forest National Park and the Šumava National Park	1.11- 2.11, distance sampling with thermal camera, density class = 2
Sweden – Koberg (SE)	58.1448 N, 12.4361E	mainly flat boreal forest interspersed with arable land and pastures	70-200	Swedish University of Agricultural Sciences (SLU)	0.8-1.71, fecal pellet distance sampling, density class = 1
Norway west (NO)	60.5880 N, 8.4220E	hilly terrain, dominated by boreal forest in valleys and tundra above treeline	200-1000	Norwegian Institute for Nature Research (NINA), and University of Oslo (UiO)	1-3, some pellet group counts and expert knowledge, density class= 2

APPENDIX 3-B. Environmental variables derived from Global Information System (GIS) layers used in the ecological distance and niche overlap estimation, and the analysis of the determinants of migration plasticity in roe deer (*Capreolus capreolus*) in five European study areas.

Covariate	Type	Reso-	Covariate Description
QUESTION 1: CLASSTIFICATION OF MIGRATION IN ECOLOGICAL SPACE			
Topography[1]			
North	Categorical	30	North aspects from 315° to 45°
South	Categorical	30	South aspects from 135° to 225°
East	Categorical	30	East aspects from 225° to 315°
West	Categorical	30	West aspects from 45° to 135°
Flat	Categorical	30	No aspect (slope = 0)
Slope	Continuous	30	Percent slope (equivalent to 0 – 90°)
Elevation	Continuous	30	Elevation in meters
Ruggedness	Continuous	30	Ruggedness in meters
Landcover[2]			
Human	Categorical	25	Continuous urban fabric, Discontinuous urban fabric, Industrial or commercial units, Road and rail networks and associated land, Port areas, Airports, Mineral extraction sites, Dump sites, Construction sites, Green urban areas, Sport and leisure facilities
Shrub	Categorical	25	Transitional woodland-shrub, Sclerophyllous vegetation, Moors and heathland, Natural grasslands
Conifer	Categorical	25	Coniferous forest
Deciduous	Categorical	25	Broad-leaved forest
Mixed	Categorical	25	Mixed forest
Agriculture	Categorical	25	Non-irrigated arable land, Permanently irrigated land, Olive groves, Annual crops associated with permanent crops, Complex cultivation patterns, Land principally occupied by agriculture, with significant areas of natural vegetation, Agro-forestry areas, Orchards, Pastures

Appendix 3-B continued

Water & Wetlands	Categorical	25	Water courses, Water bodies, Inland marshes, Peat bogs
Rocks & Ice	Categorical	25	Glaciers and permanent snow, Bare rocks
Vegetation Productivity			
NDVI[3] mean	Continuous	250	Vegetation period average NDVI between May 9th and September 14th during ordinary years and May 8th and September 13th during ordinary years
NDVI[3] SD	Continuous	250	Vegetation period standard deviation NDVI between May 9th and September 14th during ordinary years and May 8th and September 13th during ordinary years
QUESTION 2: DETERMINANTS FOR MIGRATION			
Risk Exposure			
Nightlight	Continuous	1 000	Human density
Canopy closure	Continuous	250	Canopy closure in %
Climate			
Winter severity	Continuous	250	Based on snow MODIS data, % of time a cell was covered by snow between October and March the following year.
Annual average	Continuous	1 000	Bioclim 1[4]
Spatiotemporal variation of forage resources			
Contingency	Continuous	250	Seasonality of NDVI based on 16-day NDVI rasters between 2003 and 2014.
Constancy	Continuous	250	Between-year variability of NDVI based on 16-day NDVI rasters between 2003 and 2014.
Predictability	Continuous	250	The sum of contingency and constancy
Contingency sd	Continuous	250	Standard deviation (sd) measuring the spatial variation of contingency
Constancy sd	Continuous	250	Standard deviation (sd) measuring the spatial variation of of constancy
Predictability sd	Continuous	250	Standard deviation (sd) measuring the spatial variation of of predictability

[1] CGIAR-DEM/SRTM digital elevation model (Jarvis et al. 2008) was used for latitudes less than 60° N and the NASA – ASTER relative digital elevation model (Hirano et al. 2003) with a resolution of 60m was used for latitudes of more than 60 ° N.
[2] Land-cover data was obtained from the CORINE Land Cover 2006 raster data (http://dataservice.eea.europa.eu/dataservice/).

[3] Normalized Difference Vegetation Index, Modis MOD13Q1 data, smoothing procedures based on approaches described by Maselli (2004)
[4] Bioclim / WoldClim – Global Climate Data data (Hijmans et al. 2005).

LITERATURE CITED – APPENDIX 3-B

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology **25**:1965-1978.

Maselli, F. 2004. Monitoring forest conditions in a protected Mediterranean coastal area by the analysis of multiyear NDVI data. Remote Sensing of Environment **89**:423-433.

CHAPTER 4. ASSESSING DETERMINANTS OF MIGRATORY BEHAVIOR FOR TWO LARGE HERBIVORES WITH CONTRASTING SPECIES-SPECIFIC TRAITS[3]

INTRODUCTION

Movement is one of the most fundamental features of animals and important for all ecological and evolutionary processes (Nathan et al. 2008). Seasonal movements by animals can take on many forms (Chapman et al. 2011), and migration is one of the best-described movement behaviors. Understanding migration is important, because it not only affects individuals and populations, but also alters and shapes community and ecosystem structure (Chapman et al. 2011, Bauer and Hoye 2014). In general, individuals migrate across gradients, such as altitude, latitude or rainfall that affect resource availability (Fryxell and Sinclair 1988). Partial migration, when only part of the population migrates while another remains sedentary, is the prevailing type of migration in many taxa with examples ranging from invertebrates, fish, birds to mammals (Kaitala et al. 1993, Dingle 2006, Chapman et al. 2011). Besides migratory tendency, also the patterns, such as migratory distance and timing, vary widely within populations (Cagnacci et al. 2011, Monteith et al. 2011) and individuals between years (Fieberg et al. 2008, Eggeman et al. *in review*). While several studies address factors driving migratory plasticity within the same population or species, studies addressing determinants for partial migration across multiple populations of different species are rare (Mysterud et al. 2012, Hopcraft et al. 2014). However, such

[3] This manuscript is co-authored by M. Hebblewhite, F. Cagnacci, A. Mysterud, F. Focardi and other EURODEER group members with intention to submit Journal of Animal Ecology.

comparisons are needed if we are to understand the general drivers of migration across species and ecosystems (Bolger et al. 2008).

Large herbivores are one taxonomic group of economic and ecological importance (Hobbs 1996, Gordon et al. 2004) for which an improved understanding of the drivers of migration is sorely needed (Bolger et al. 2008). The conservation of ungulate migration has received considerable attention recently, sparked by widespread declines in many migratory ungulates (Berger 2004, Bolger et al. 2008). Ungulate ecology and life-history are driven by bottom-up nutritional effects through forage and top-down effects through predation (Senft et al. 1987). Many ungulates undergo migration between seasonal ranges, often associated with plant phenology and weather (Mysterud et al. 2001, Sawyer and Kauffman 2011, Bischof et al. 2012), and many ungulate populations are also partially migratory. Ungulate migration is thought to be a strategy to escape the adverse effects of snow during winter in the northern hemisphere (Nelson 1995) that limits access to forage and increases the cost of locomotion (Parker et al. 1984, Ball et al. 2001). According to the forage maturation hypothesis (FMH), the leading hypothesis for ungulate spring migration, ungulates migrate to gain access to high quality forage during summer (Albon and Langvatn 1992, Hebblewhite et al. 2008). Alternative, but non-exclusive hypotheses include reduced exposure to predation risk (Fryxell and Sinclair 1988, Skov et al. 2011), anthropogenic threats (Fryxell et al. 2008, Singh et al. 2012), and inter- or intraspecific competition (Mysterud et al. 2011). Despite these alternative hypotheses, the primary driver of seasonal migration is thought to be forage resource variability in seasonal migration (Mueller and Fagan 2008).

Forage resources can vary dramatically across spatiotemporal scales in seasonal environments, leading to wide variation in migratory behavior (Mueller and Fagan 2008, Mueller et al. 2011). For example, migration is predicted to be highest in landscapes with regular, seasonal fluctuations in environmental conditions, where animals may migrate in response to seasonal cues (Sabine et al. 2002, Berbert and Fagan 2012), while landscapes that show very little spatiotemporal resource variation should support sedentary populations (Jonzén et al. 2011). Consequently, the proportion of migrants in a population is expected to increase with latitude and altitude due to increasing snow, decreasing forage and overall higher temporal predictability (i.e. seasonality) in temperate environments (Singh et al. 2014, Mueller et al. 2011). Between the two extremes of obligatory migration and residency, migration behavior may be very plastic in response to favorable conditions and stochastic events (Cagnacci et al. 2011). There is also great variability at the individual-level in timing or distance of migration. For example, Teitelbaum et al. (2015) showed that across 94 large herbivores, migration distance was determined by resource availability and the spatial scale of resource variability.

Few studies have examined the link between resource variability and migration probability, distance and timing for multiple large herbivores spanning a similar latitudinal gradient (Mueller et al. 2011). Mysterud et al. (2012) compared the proportion of migrants within sympatric red- (*Cervus elaphus*) and roe- (*Capreolus capreolus*) deer populations in Norway and, surprisingly, found large differences with 94% of red deer but only 24% of roe deer being migratory. Since environmental conditions were similar they suggested that multiple causes affected migration in these two species. Similarly,

Hopcraft et al. (2014) showed that two sympatric large herbivores, wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*), responded to different environmental cues in the same landscape. Wildebeest tended to move in response to forage quality more or less regardless of predation risk, while zebra traded-off predation risk and access to high-quality forage. Lastly, pronounced differences between sexes of the same species, especially in sexually dimorphic ungulates (Kie and Bowyer 1999, Bowyer 2004), should be incorporated when studying migration. Differences between the two sexes may arise from varying allometry and species-specific traits (e.g., reproductive strategies; Clutton-Brock et al. 1982, Hamel et al. 2010). Overall, comparative approaches can provide valuable insights into the mechanistic drivers of migration between species, populations and sexes.

Herein, we examine migratory behavior for two partially migratory ungulate species, roe deer and red deer, spanning a similar latitudinal gradient from the southernmost European populations in Italy and northernmost populations in Norway (Fig.4-1). We first tested how migratory behavior differs amongst > 500 Global Positioning System (GPS) collared individuals in 10 roe and 12 red deer populations across Europe. We tested for differences in the probability of migration, the distance and the timing between species, populations and sexes. Next, we examined the relative contributions of abiotic and biotic factors and their spatiotemporal variability on structuring plasticity in red and roe deer across similar latitudinal gradients. Herein, we develop our predictions of differences between species, sexes and populations.

Predictions

Roe and red deer are common throughout Europe (Mysterud et al. 2012), spanning a broad range of habitats (Mitchell-Jones et al. 1999) with often overlapping distributions. Despite their similarities, these two species occupy different niches (here: the Eltonian niche; Elton 1927) due to differences in feeding behavior, sociality or breeding behavior, and we hypothesize differences in migratory behavior. Red deer are larger (average female weight: 108 kg; Loison et al. 1999), sexually dimorphic, capital breeding, group-living, polygynous ungulates with strong female philopatry and males that hold harems during the rut in September - October (Nussey et al. 2005, Moyes et al. 2006). The much smaller roe deer (average female weight: 27 kg; Loison et al. 1999) are income breeding, weakly polygynous and more solitary ungulates, with a male-territorial breeding system with the rut occurring in July and August (Vanpe et al. 2009). Cagnacci et al. (2011) studied migratory plasticity in roe deer across Europe and found wide variation in the proportion of migratory individuals, the distance and time they migrated across populations. In contrast, little is known about migration plasticity in red deer across a wide latitudinal gradient, but research in individual populations or countries also suggests variation in migratory behavior (Bocci et al. 2010, Mysterud et al. 2011, Zweifel-Schielly et al. 2012). Consequently, we expected the following between species, sex, and population differences in migratory behavior (Table 4-1).

Between species, migration behavior may be shaped by multiple different causes in each species (Mysterud et al. 2012). While forage maturation should affect energetic intake rates in all ruminants, the magnitude of the effects should be greatest in grazers and lowest in browsers (Owensmith and Novellie 1982, Fryxell 1991,

Mysterud et al. 2012), because grass phenology is more strongly seasonal than browse (Hebblewhite et al. 2008). Red deer are classified as generalists with a mixed diet of grasses, forbs and shrubs (Hofmann 1989), whereas roe deer are browsing concentrate selectors (Verheyden et al. 2011). Therefore, we predicted that the proportion of migrants will be higher in red deer than roe deer (Table 4-1; P_{F1}). We also expected that the timing of migration by red deer would be more strongly tied to herbaceous (graminoid and forb) phenology than the timing by roe deer (Table 4-1; $P_{T1.1}$; Albon and Langvatn 1992, Nicholson et al. 1997, Mysterud 1999). We expected the timing of spring migration to be later for red deer than for roe deer due to an often delayed green-up of graminoids compared to forbs (Table 4-1; $P_{T1.1;}$ Hebblewhite et al. 2008). In contrast, graminoids commonly cure before forbs and shrubs in autumn (Hebblewhite et al. 2008) and may drive earlier initiation of autumn migration in red deer (Table 4-1; $P_{T1.2}$). We also predicted roe deer autumn migration to be stronger driven by snow due to their much smaller body size and associated locomotive constraints rather than forage (Table 4-1; $P_{T1.2}$). In terms of distance, we predicted red deer to migrate farther than roe deer due to their larger body size (P_{D1}, allometric scaling; Eisenberg 1983).

We also expected differences between sexes in migratory behavior between red- and roe deer. We predicted roe deer males to initiate spring migrations sooner than roe deer females and red deer to establish male territories on summer range as soon as possible (e.g. Table 4-1, P_{T2}; arrival time hypothesis; Ketterson and Nolan 1976). Consequently, male roe deer are also expected to initiate autumn migrations later than roe deer females or red deer due to male territoriality and the much earlier

breeding season of roe deer compared to red deer (Table 4-1, P_{T2}). In general though, we expected fewer differences in the frequency of migration between roe-deer males and females due to low sexual dimorphism compared to red deer males and females (P_{F2}; Bowyer 2004).

At the between-population scale, we predicted that migratory behavior would be more prevalent (higher frequency of migrants) in more seasonal landscapes such as at higher latitudes and altitudes (Table 4-1, P_{F3}). We also predicted that the timing of migration would be delayed at northern latitudes in spring and occur earlier in autumn (Table 4-1, P_{T3}). Overall, we expected the timing of spring migration to be influenced by forage green-up (Bischof et al. 2012, Lendrum et al. 2013), while increasing snow depth and decreasing temperatures have been reported as main trigger for autumn migration (Sabine et al. 2002). Consequently, we predicted that the overall probability of migration for both species would also increase with winter severity and timing in spring and autumn would correlate with green-up and snow (P_{T4}), respectively. We also expected that if landscapes were more seasonal and predictable between years (e.g. forage green-up), migration should be more common (P_{F3}). Finally, we predicted that the distance of migration should be further at northern latitudes (Singh et al. 2012), but shorter in steep terrain due to increased topographic and associated forage diversity as well as increased cost moving in rugged landscapes (P_{D2}; Levey and Stiles 1992).

METHODS

Animal Location Data

Our 10 roe deer and 12 red deer populations spanned the same latitudinal gradient (Fig. 4-1), and over 500 GPS radio-collared individuals. For a detailed comparison of study area characteristics and sample sizes see Appendices 4-A (roe deer) and 4-B (red deer). At the northernmost extent we used roe deer GPS data collected in southern Norway in a hilly area characterized by boreal forests in valleys and tundra at higher elevations. The northernmost red deer GPS collar data was collected in Sunnfjord in western Norway (SW) close to the coast in the boreonemoral zone dominated by deciduous forests and Scots pine (*Pinus sylvestris*) forests. Another Norwegian population was in Buskerud (SE) in the southern boreal zone with coniferous forests composed of Norway spruce (*Picea abies*) and Scots pine. The only Swedish roe deer population was near Koberg in flat terrain and about 70% boreal forest cover as well as about 20% pastures. The red deer monitored in Sweden were in a southern area partly covered by agricultural land. Denmark red deer dwelled in a typical prairie environment, with reduced cover. Roe deer in Poland were monitored in Bialowieza National Park characterized by lowland primeval forest. The only Austrian roe deer population considered in this study occurs in Alpine habitat with coniferous forests. The northern German red deer population occurs in forest habitat interspersed with agricultural lands in flat terrain. South-eastern German red- and roe deer populations were sympatric on the border of Germany and the Czech Republic in central European sub-mountainous forests and intermediate elevations. The population of roe deer located in southwestern Germany can be classified as hilly with forested habitat interspersed with arable land and meadows. Roe deer in France were monitored in a fragmented agricultural landscape with open fields and patches of Mediterranean forest (Aurignac). The French red deer population

was instead studied in a more forested and mountainous landscape typical of the Pyrenees region and Cavennes. The southernmost study area for red deer was in Stelvio National Park, in northern Italy characterized by rouged terrain and mountains up to 3 900 m with a predominantly coniferous vegetation. In close proximity were the two northern Italian roe deer population of which Italy 1, Val Rendena, is characterized by very diverse Alpine habitats with elevations up to 2 200 m and Italy 2, Monte Bondone, is another Alpine population characterized by slightly lower elevations.

Animals were captured using a variety of methods including box trapping and drive netting for roe deer, and ground darting for red deer under approved animal care protocols from the respective regions and countries (e.g., University of Montana animal care protocols, AUP 060-12MHWB-113012 for roe deer in population Italy 1). Following capture, individuals were marked with GPS radio-collars. Details on capture dates and GPS collars can be found in Appendix 4-C. The GPS data were screened for errors using a standard procedure based on animal movement theory (Bjorneraas et al. 2010). Average fix success was high, i.e. 0.94 (SD=0.09) for roe deer and 0.96 (SD=0.12) for red deer (Appendix 4-C), obviating the need to be concerned with GPS bias (Frair et al. 2010).

Classification of Migration Strategies

To classify all animals into residents and migrants we used GPS location data collected between February 15th of the first year and February 14th of the following year. If animals were monitored for multiple years they were treated as separate migration years and migration strategy was allowed to vary between years (e.g., as observed by Eggeman et al. *in revision*). We censored animals with discontinuous

GPS datasets that had gaps of more than one month. Also, we only included individuals with sufficiently long (≥10 months) sampling periods that allowed reliable identification of seasonal space use patterns. Because animal location data were collected with varying sampling intervals ranging from <15 minutes to 12 hours, we averaged location data to one observation per day.

Because it has been shown that migration classification methods show a substantial amount of disagreement between them (Cagnacci et al. *in revision*), we classified all individual red- and roe deer using a combination of methods, including the net-squared displacement (NSD; Bunnefeld et al. 2011) and a supervised spatial clustering method (Cagnacci et al. 2011, Cagnacci et al. *in revision*). The NSD assesses the cumulative squared displacement from the initial starting location and then five movement models, i.e. resident, migrant, mixed migrant, nomad and disperser, are fit to these trajectories using non-linear models (Bunnefeld et al. 2011). We selected the best movement model for each animal-year using AIC (Burnham and Anderson 2002). Because we were primarily interested in migration events versus resident behavior, we excluded the nomad model and pooled mixed migrants and migrants in our analyses. Using the NSD classifications as described by Bunnefeld et al. (2011) mixed migrants are still migratory animals, but return to a slightly different winter range. We compared the NSD classification with the results from supervised spatial clustering algorithm described in Cagnacci et al. (2011) that classifies animals as either resident with only one annual range or migratory (i.e. with multiple ranges). If animal classifications were different in both methods we visually inspected movement trajectories and assigned a movement strategy (Bischof et al. 2012).

Overall, this combination of methods allowed us to define animals as migrants according to the following criteria: migrants needed to have non-overlapping seasonal ranges for a minimum of one month (i.e. residence time >30 days) and animals were not dispersers. Red deer (Jarnemo 2008, Stopher et al. 2011) and roe deer (Debeffe et al. 2014) may use different breeding areas than their summer and winter ranges and factors affecting these excursions and late summer migrations are presumably different from factors driving spring migrations. Therefore, we excluded all animals that conducted migrations from winter to summer range after July 15th from our subsequent analyses (Fig. 4-4). Once animals were classified as either two of the strategies, we extracted the timing of spring and autumn migration events, the Euclidean migration distance by refitting the NSD functions for migration and residency.

Statistical Analyses

To explain migration probability, migration distance and factors affecting migration timing for red and roe deer we employed a manual stepwise model building process (Hosmer and Lemeshow 2000) to create the most parsimonious models using different statistical methods for each question. We determined our top models based on the Akaike Information Criterion for small sample sizes (AICc; Burnham and Anderson 2002). We considered environmental covariates (see Environmental Covariate section below) that were previously reported to influence partial migration in ungulates. We standardized all continuous covariates (Gelman 2008), allowing covariate effect sizes to be comparable to factors (e.g. sex). All covariates were screened for collinearity using the Pearson's correlation coefficient threshold of $| r | > 0.6$ for variable removal (Hosmer and

Lemeshow 2000). We retained the variable with the lower log-likelihood, highest coefficient of determination (pseudo R^2) and lowest p-values (Boyce et al. 2002). We first conducted univariate analysis, using a $p<0.25$ on a Wald ch^2-statistic as a cut-off for the inclusion in subsequent model building. To test whether coefficients were nonlinear we explored covariates using semi-parametric Generalized Additive Models (GAMs; Hastie and Tibshirani 1990), and either transformed coefficients or used quadratics to describe non-linear patterns (Hosmer and Lemeshow 2000). All proportions were arcsine square-root transformed. Retained variables entered the multivariate logistic regression modeling process to build a small subset of biologically sensible candidate models (Hosmer and Lemeshow 2000). We considered all biologically meaningful interactions. Because 8% of the roe and 24% of the red deer observations were on animals that were sampled more than one year, we also tried to include a random intercept for individual repeated measures (Gillies et al. 2006). But, because individual migratory behavior can vary between years (Fieberg et al. 2008, Eggeman et al. *in review*), and, because few individuals were monitored multiple years, there was often little support for individual random effects. To understand if there were important study area differences we tested for significance of random effects for study area in our models using mixed models (Gillies et al. 2006). We tested models for assumptions of linearity, influential points as well as homogeneity of variance (Zuur et al. 2009). We present and rank models within two AIC_c units (ΔAIC_c) of the best ranked model to avoid inclusion of uninformative parameters (Arnold 2010). We considered a model if the parameters in the top model were not just a subset of those of the competing model (Burnham and Anderson 2002, Arnold 2010). If top models were mixed models, we report both mixed and fixed models

and those may be > 2 ΔAIC_c apart. In general, we evaluated model goodness of fit with internal model diagnostics. We also present the likelihood-ratio based pseudo-R-squared (R^2; Nagelkerke 1991). All statistical analyses were performed in program R, version 3.1.2 (R Development Core Team 2013).

Migration Probability

We first assessed general differences in the frequency of migration within and between red- and roe deer (Table 4-1). We created the most parsimonious generalized linear models (GLM) with a binomial family and log link contrasting migrant (1) and resident (0) animals for each species (Hosmer and Lemeshow 2000). We also tested for significant random effects of study area using generalized logistic mixed-effects models (GLMM) with a random intercept for populations (Gillies et al. 2006). Specifically, we tested which factors experienced by an animal on its winter range were related to the probability of migration in a given year (Singh et al. 2012). To standardize covariate sampling for each individual, we used equally sized sampling ranges for all animals within a species by sampling the radius of the average resident home range size using the average home range radius of the intercept coefficient of the resident NSD model (Nielsen et al. 2014), which was r = 0.79 km (SD=0.51; 1.96 km^2) for roe deer and r = 1.12 km (SD=0.84; 3.94 km^2) for red deer. Then, we followed recommendations by Bowyer and Kie (2006) and used a standardized shape to set the range for sampling of habitat variables. We sampled environmental covariates (see Environmental Covariate section below) within the area centered on the centroid of all winter (January to March) GPS locations using the QGIS ver. 2.10 (QGIS Development Team 2014). If we monitored a deer for more than one year we used the centers for each winter range and

calculated the variables unique to the each winter range. We calculated the average of all continuous environmental variables and the proportion of all categorical variables. Broadly, we tested how the following covariates measured on winter ranges affected the probability of migration; the effects of weather (average snow depth, average temperature), vegetation and its predictability (contingency, constancy), terrain (slope, elevation) and risk (nightlights and canopy closure).

Migration Distance

We first tested for overall differences between species using ANCOVA on log-transformed migration distance. Second, we tested our hypotheses about factors affecting migration distance within species. The distribution of migration distances were strongly left-skewed and we therefore evaluated suitability of Poisson, negative binomial or GLM with a log-transformed distance by comparing the conditional mean and variance of the dependent variable (Venables and Ripley 2002). We tested for overdispersion in our data using R-package "AER" (Kleiber and Zeileis 2008) and decided to use negative binomial models to test which factors effect migration distance for roe-and red deer. For migration distance we did not include random effects for the study area, because the number of migrants was very low in some study areas and did not justify an increase in model complexity. We used the same covariates sampled on roe-and red deer winter ranges as for the probability of migration described above.

Migration Timing

We first explored broad differences in the timing (Julian dates) of fall and spring migration between species and sexes using ANCOVA. To model differences in migration

timing we used time-to-event models with a log-link to determine the daily probability of site fidelity (i.e. the negative cumulative migration probability) as a function of different time-varying covariates as well as averaged covariates on seasonal ranges for each individual animal (Fieberg et al. 2008). We used semi-parametric Cox proportional hazards (PH) models (Cox 1972):

$$h(t|x_j) = h_0(t)exp^{\beta x}, t > 0,$$

where h(t|xj) describes the instantaneous negative probability of migrating (hazard rate) at time t given risk covariate values x_j for deer j with model coefficients βx. The baseline hazard function $h_0(t)$ describes how the probability of migration per time unit changes over time at baseline or reference levels of covariates. The Cox-proportional hazard (PH) uses a multiplicative hazard ratio ($exp^{\beta x}$) to compare hazards among categorical variables and to estimate the effect of continuous covariates on the baseline hazard rate. Lastly, we used the Andersen-Gill formulation of the Cox PH model, based on counting process theory (Andersen and Gill 1982, Therneau and Grambsch 2000), to accommodate time-varying covariates and left and right staggered entry and exit (Pollock et al. 1989). We used Martingale residuals to detect model outliers (Hosmer et al. 2008) and tested for non-proportionality in PH models using the scaled Schoenfeld residuals (Hosmer et al. 2008). We assessed the proportionality of factors by graphing the log hazard against ln(t), and examined whether the lines for the levels (e.g., male, female) within factors were parallel (Therneau and Grambsch 2000).

Broadly, we accounted for effects of weather and vegetation phenology as time-varying covariates, phenological predictability (contingency, constancy), terrain,

risk (nightlights and canopy closure) and latitude averaged on seasonal ranges (see Environmental Covariate section below). We used sex as an intrinsic predictor variable. For spring migrations, the encounter history of an individual started on February 1st or the earliest date data were available, but before a spring migration event occurred and continued until the individual migration event occurred. For autumn the encounter history of an individual started on June 1st before the first autumn migration event occurred and continued until the individual migration event occurred. Resident animals remained in the dataset until one day after the last migration event occurred and where finally censored. We also tested for random study area effects accounting for among-group heterogeneity in migration probability within each of the 10 roe deer and 12 red deer study areas using shared frailty (Cleves et al. 2002, Hosmer et al. 2008). The inclusion of a shared frailty term allows valid population-level inferences across populations and if frailty was significant, we report population-averaged covariate effects (Cleves et al. 2002). For descriptive purposes, we estimated migration curves for sex and study areas using the Generalized Kaplan-Meier (KM) estimator and compared their significance using Mantel-Haenszel test (Pollock et al. 1989). We estimated KM survival rates and Cox PH models using the R package 'survival' (Therneau 2015).

Environmental Covariates

We derived spatial environmental covariates measuring vegetation cover and variability, snow, topography and other hypothesized drivers of migratory behavior in two ways. First, we examined seasonal averages for covariates for individuals for the probability and distance of migration analyses above. Second, for the question of the

timing of migration, we derived time-varying environmental covariates matched with each GPS location. To characterize forage productivity and its variability we used the Normalized Difference Vegetation Index (NDVI), a remotely-sensed measure of vegetation greenness demonstrated to provide an index of habitat productivity for large herbivores (Pettorelli et al. 2005, Hamel et al. 2009). We used NDVI data that were smoothed using an operational processing chain with a Whittaker smoother removing large parts of the noise and leading to reliable and consistent NDVI products with a weekly updating interval and well characterized errors (Vuolo et al. 2012). We considered the mean NDVI during the growing season (from May to September) as a static variable at the seasonal-range level in the analysis of the probability of migration and migration distance during the same year the animal location data were collected. For the time-to-event analyses, we also used NDVI as a time-varying variable linked to each animal GPS location. Because we expected deer to respond to progressive changes in NDVI, we also calculated a metric of change in NDVI by taking the difference in the time-matched NDVI at time t to the NDVI two weeks prior to time t (delta NDVI; ΔNDVI).

To characterize temporal and spatial variability we used constancy (C) and contingency (M) indices described by Colwell (1974). We applied his definitions to vegetation productivity, namely NDVI between 2003 and 2014. Constancy indicates to what degree vegetation phenology is the same for all months and all years. High constancy means that the NDVI fluctuations between 2003 and 2014 were very low within months and between years for a given pixel (i.e. vegetation cover changes very little overall). High constancy implies high predictability in environments with little or no

seasonality. Contingency (M) describes how closely certain phenological states correspond to time periods across years, i.e. it is the degree to which NDVI values during one year were the same during all other years during the same period (i.e. month). Thus, it indicates if there are strong periodicities in the data and is maximized if patterns are similar across years. Thus, landscapes with a high degree of seasonality may be very predictable (low constancy combined with high contingency), or unpredictable (low constancy with low contingency), which warrants fitting an interaction term between both. To calculate contingency and constancy we used monthly averages of NDVI. NDVI values range from 0 to 1 and we grouped NDVI those into 10 equal interval bins between 2003 and 2014. Negative values were reclassified as 0 (English et al. 2012).

To characterize climate in our red and roe deer study areas we used interpolated meteorological data of daily mean temperature (C), precipitation (mm) and snow depth (cm) using Agri4cast data (http://agri4cast.jrc.ec.europa.eu/DataPortal/). These data interpolate weather station data that are limited to stations that regularly collected data in near real time at a resolution of 25 km (Burrill and Vossen 1992). We averaged these daily data and calculated their standard deviation (SD) for each deer range between January and March to characterize average winter conditions in the analysis on the probability of migration and the distance of migration. For the time-to-event modeling we paired each animal GPS location with daily weather data. Because daily snow depth data was incomplete for some deer, we used presence/absence data of snow cover, MOD10A2 16-day composite maximum snow extent data at a resolution of 250m (Hall et al. 2000) and calculated the snow cover extent across all daily GPS locations for each deer (%).

To characterize risk (e.g. risk of human hunting or disturbance; Singh et al. 2011), we used the proxies nightlights and canopy closure. The nightlights index has been used to describe the level of human activity (Small et al. 2005, Morellet et al. 2013). Canopy has been shown to have important benefits for deer as concealment cover (Lone et al. 2014, Lone et al. 2015) as well as thermoregulation (Dussault et al. 2004) and in general is a proxy for the proportion of forest within deer ranges. We used global forest change data of canopy closure at a resolution of 250 m averaged in each deer range (Hansen et al. 2013). Lastly, because agricultural subsidies have been shown to affect migration (Wilmers and Levi 2013), we estimate the percentage of agriculture in each deer range using EEA-Corine Landcover (CLC; www.eea.europa.eu/data-and-maps/data/corine-land-cover-2000-2006). Spatial data management was conducted using a PostgreSQL 8.4.1 PostGIS 1.5.2 (www.postgresql.org/; http://postgis.refractions.net/) spatial data base and QGIS 2.4.0 software (QGIS Development Team 2014).

RESULTS

Classification of Migration Strategies

We identified 51 roe deer as migrants, 20 as dispersers and 222 as residents in 10 study areas using the combined approach of NSD (Bunnefeld et al. 2011) and the spatial clustering method (Cagnacci et al. 2011, Cagnacci et al. *in revision;* Figure 4-1; Appendix 4-A). For red deer we identified resident 141 migratory, 8 dispersing, and 123 residents in 12 study areas (Figure 4-1; Appendix 4-B). We removed dispersing animals from subsequent analyses. We found statistically significant differences in the baseline probability of migration between roe and red deer across Europe (X^2=72.13, N=537, p< 0.001, Fig. 4-2; P_{F1}). Red deer were more than three times more likely to migrate than roe

deer, with 60% of all red deer being migratory compared to only 19% of all roe deer (Fig. 4-2). Only red deer differed between sexes in migratory probability, where red deer males had a higher probability of migration than females red deer: $X^2 = 47.67$, N = 264, p< 0.001; roe deer: $X^2 = 2.29$, N = 273, p = 0.13; Fig.4-2; P_{F2}).

Migration Probability

We identified two competing models explaining the probability of migration for roe deer and one model for red deer (Table 4-2). All models contained an interaction between average snow cover on the winter range (herein snow cover) and slope (Fig.4-3; P_{F3}). The first model explaining roe deer migration probability was a function of the average NDVI within roe deer winter ranges (β = 1.39, SE = 0.53) in addition to the interaction term of snow cover and slope (β = -1.34, SE = 0.68) and the main effects for the average snow cover (β = 1.14, SE = 0.42) and slope (β = 0.87; SE = 0.32 , Table 4-3). Interestingly higher summer NDVI values on winter range predicted a higher probability to migrate. The second roe deer model included % forest on the winter range besides the interaction of snow cover and slope and more forest cover increased the probability of migration (β = 0.94, SE = 0.34). These two most parsimonious models explaining roe deer migration probability had an adjusted R^2 of 0.22 (model 1) and 0.18 (model 2; Table 4.-2). The area under the receiver operator curve (AUC) was 0.773 and 0.783.

The most parsimonious model explaining red deer migration included nightlights (β = 1.86, SE = 0.60), indicating that human activity increases the probability of migration for red deer. As expected red deer stags had a higher probability of migration compared to females (β = 1.49, SE = 0.40; Fig. 4-2, Table 4-3). The coefficients for the interaction term between snow cover and slope and their main effects indicted the same

direction for the probability of migration as for roe deer, but the effect was much stronger (i.e. β for interaction term = -5.30, SE = 1.30; Table 4-5, Fig. 4-3). The marginal R^2, indicating the variance explained by fixed factors, for the most parsimonious red deer migration model was 0.32 and the conditional R^2, indicating the variance explained for fixed and random factors was 0.60. Thus there was a lot of variance explained in the top model by the random intercept for population-level differences in migratory propensity (Table 4-3).

Migration Distance

Roe deer migrated on average shorter distances than red deer (μ_{roe} = 6.13 km, SD = 7.61 km; μ_{red} = 12.13 km, SD = 12.12 km; ANCOVA, N = 192, F = 12.545, p<0.001; P_{D1}). We found no statistically significant differences between the sexes of both species (i.e. p>0.1). The most parsimonious model explaining roe deer migration distance included slope and nightlights, where steeper terrain increased migration distance (β = 0.71, SE = 0.41) and increasing human presence (i.e. nightlights) decreased migration distance (β = -0.69, SE = 0.37) of roe deer (Tables 4-4 and 4-6). The roe deer migration distance model had an adjusted R^2 of 0.21. Red deer migration distance was best explained by two competing models (Tables 4-4). The first model predicted increasing migration distances with latitude (β = 0.60, SE = 0.13), increased variability of temperature on winter range (SD temperature; β = 0.35, SE = 0.13) and decreasing migration distances with increasing canopy closure (β = -0.34, SE = 0.14; Table 4-5). Thus, our predictions (Table 4-1) were only partially supported, because migration distance increased with latitude for red deer only and in contrast to what we expected increased with slope for roe deer (P_{D2}). Interestingly, nightlights (β = 0.37, SE = 0.14)

had an opposite effect on red deer migration distances compared to roe deer migration distances, but the coefficient for nightlights was only marginally significant for roe deer. The second red deer model included contingency (i.e. seasonality), which had a positive effect on migration distance ($\beta = 0.40$, SE = 0.14). The first red deer migration distance model had an adjusted R^2 of 0.40 and similarly, the second model explained 39% of the variation according to R^2.

Migration Timing

The log-rank test for between species differences in the daily probability of migration indicated statistically significant differences in spring and autumn (log rank spring: $X^2 = 68.1$, 1df, $p<0.001$; log rank autumn: $X^2 = 78.9$, 1df, $p<0.001$). When looking at the average migration dates for both species, roe deer migrated sooner than red deer in spring (Fig. 4-4; all means are Julian dates: $\mu_{roe} = 130$, i.e., May 10, SD = 53.8; $\mu_{red} = 144$, i.e., May 24, SD = 40.5; ANCOVA, N = 192, $F = 12.55$, $p=<0.001$; $P_{T1.1,}$ P_{T2}) and later in autumn ($\mu_{roe} = 309$, i.e., November 4, SD = 50.0; $\mu_{red} = 278$, i.e., October 10, SD = 38.1; ANCOVA, N = 192, $F = 10.95$, $p=0.001$). We found no sex-specific differences in daily migration probability for roe deer in spring or autumn (Log-rank spring: $X^2 = 0.1$, 1df, p = 0.708; Log rank autumn: $X^2 = 0.1$, 1df, p = 0.842; Fig. 4-4). Female roe deer migrated before males, but variation was much higher for males and differences not statistically significant ($\mu_f = 126$, SD=35.60; $\mu_m = 136$, SD = 72.90; ANCOVA, N = 51, $F = 0.020$, p = 0.875; Fig. 4-4). Roe deer females initiated autumn return migrations 24 days sooner than males ($\mu_f = 291$, SD = 48.07; $\mu_m = 315$, SD = 51.01; ANCOVA, N=51, $F = 2.907$, p = 0.094; Fig. 4-4; P_{T2}). The log rank test for sex-specific differences between red deer females and red deer males was significant for both seasons (Log rank

spring: X^2 = 5.1, 1df, p = 0.024; Log rank autumn: X^2 = 4.3, 1df, p = 0.037; Fig. 4-5). Red deer females migrated 29 days sooner than males in spring (μ_f = 134, SD = 29.69; μ_m =163, SD = 51.78; ANCOVA, N = 141, *F* = 19.571, p<0.001), but around the same time in autumn (μ_f = 276, SD = 34.66; μ_m = 281, SD=44.42; ANCOVA, N= 141, *F* = 0.720, p = 0.370; Fig. 4-4). Individuals of both species that migrated further did initiate migration sooner than animals that migrated to closer summer ranges (roe deer: β = -2.5e-03, SE = 8.4e-04; *F* = 9.517, p = 0.003; red deer: β = -6.6e-04, SE = 2.4e-04; *F* = 7.176, p = 0.008). Lastly, differences in the daily probability of migration in spring and autumn between study areas were significant for both seasons and species (log rank spring roe deer: X^2 = 54.1, 9 df, p< 0.001; log rank autumn roe deer: X^2 = 60.3, 9 df, p<0.001, log rank spring red deer: X^2 = 84.3, 11 df, p<0.001; log rank autumn red deer: X^2 = 137, 11df, p<0.001). Patterns seemed to follow latitudinal gradients with later migrations at northern latitudes in regions of higher seasonality in spring and earlier migrations in autumn (Fig. 4-6 and 4-7; P_{T3}).

Environmental factors affecting the daily probability of spring migration in roe deer included time-varying NDVI, the change in NDVI (ΔNDVI), and the averaged slope, elevation and nightlights on the winter range based on the two top models within two ΔAICc (Table 4-6; P_{T4}). Interestingly, as absolute NDVI increased (HR = 0.27, model 1), the daily probability of departure from winter range decreased. In contrast, a positive ΔNDVI (HR = 2.31, model 1) increased the daily "risk" of departure from winter range, suggesting that not the absolute value in NDVI initiates migration, but rather the rate of change (confirmed by the much higher HR; Table 4-7; P_{T4}). Steeper slopes (HR = 2.28, model 1) and higher altitudes (HR = 2.51, model 2, P_{F3}), denser canopy (HR = 2.63,

model 1) as well as increased human presence (nightlights, HR = 1.80, model 2) averaged on winter range increased the probability of daily 'hazard' of migration. In autumn the daily probability of roe deer migration from summer to winter range decreased with higher values of NDVI (HR = 0.28, model 1; please note that ΔNDVI found no significant support p = 0.91). Further, the daily probability of autumn migration increased with seasonality of the summer range (HR contingency = 1.82, model1; P_{F1}) and was lower for male roe deer than for females (HR = 0.66, model 2; Table 4-7, Fig. 4-4 and 4-5; P_{T2}).

The daily probability of red deer migration from winter to summer range increased with positive changes in NDVI (HR ΔNDVI = 1.25) and decreasing levels of snow (HR % snow = 0.63; Table 4-7; P_{T4}). Further, contingency (seasonality) increased the daily "risk" of migration in the spring for red deer (HR = 1.81). Lastly, the most parsimonious model describing spring migration for red deer suggested that males had a higher daily probability of migrating than females (HR = 1.52). In autumn decreasing values of absolute NDVI (HR = 0.40) increased the daily probability of migration and similarly to spring, males had a higher daily probability to initiate return movements from summer to winter ranges than females (HR = 2.37). Red deer in more constant environments had a lower daily probability of migrating in autumn (HR constancy= 0.85; P_{F1}). The daily probability of migration in autumn was not significantly affected by increasing snow depths or decreasing temperatures as predicted ($P_{T1.1}$, $P_{T1.2}$).

Including frailty improved model fit over the fixed effect survival model only for red deer migration models (spring ΔAIC of the top-ranked model without frailty = 80; autumn ΔAIC of the top-ranked model without frailty = 60.6; although this test is

potentially optimistic; Cleves et l. 2002). The variance in the probability of migration among study areas was significant for both seasons for red deer confirming substantial within-study-area correlation in migration probability. For both roe deer models we found no significant effect of between study area effects (e.g. frailty $p = 0.95$).

DISCUSSION

Our work supports our overall hypothesis that differences in migratory behavior of red and roe deer are related to differences in their species-specific traits, such as body size and breeding behavior. Red deer were more than three times as likely to migrate as roe deer. This is consistent with the FMH, which predicts a higher probability of migration for red deer due to their herbaceous foraging strategy (Mysterud et al. 2012; Table 4-1). Graminoid phenology is generally more seasonal than browse and ungulates which rely on grasses and mixed forage may need to track these resources more (Owensmith and Novellie 1982, Fryxell 1991, Hopcraft et al. 2014). We also found important differences between sexes of both species that may be related to their different social behavioral systems. In agreement with findings by Cagnacci et al. (2011), migration frequency was the same for both sexes in roe deer, potentially due to their low sexual dimorphism. In contrast, we identified approximately twice as many migrations performed by red deer males than females. This is consistent with the hypothesis that long-distance movements of the larger body sized males in polygynous mating species are driven more by reproduction than forage (Bowyer 2004). Red deer also migrated almost twice as far as roe deer, as predicted by their larger body size (Hein et al. 2012), but we found no differences between sexes in migratory distance. Consistent with red deer migration being more tied to the green-up of herbaceous vegetation, red deer migrated later than roe

deer in the spring, and earlier in the autumn. However, despite the much lower probability of migration in roe deer, we found that roe deer timing of migration also coincided with forage covariates. This suggests that forage contributes to the multiple causations that affect roe deer migration to some degree, but possibly less than for red deer. Lastly, we found substantial variation in the environmental covariates driving migratory behavior (frequency, distance, and timing) and variation between populations in migratory behavior, which highlights the plasticity of all aspects of large herbivore migration.

Migratory frequency was also affected by topography and snow cover, similar to many other studies of large herbivores (Nelson 1998, Cagnacci et al. 2011, Grovenburg et al. 2011). In our study the probability of migration was a function of the interaction between steepness and snow cover for both study species. Both species were more likely to migrate as snow cover increased, but only in flat or medium sloped study areas. Deer inhabiting steep winter ranges (mountains) had an overall high baseline probability of migration (> 50%), but the probability of migration decreased as snow cover increased, especially for red deer (Fig. 4-3). Nicholson et al. (1997) observed that some mule deer (*Odocoileus hemionus*) stayed on south-facing steep slopes at > 3 000 m elevation throughout winter with much lower snow depths than at north facing slopes in the same region. Also, Ossi et al. (2015) showed that roe deer in mountainous habitat were selective for steep slopes that had overall lower snow depths than the surrounding areas, suggesting that roe deer in such severe habitats are selective at fine scales. Thus, steep areas may provide some limited high-elevation winter habitats. In these steep, snowy environments, deer may already overwinter in high quality summer forage ranges with no

need to migrate to benefit from forage phenology in the summer. It is also possible that populations in mountainous regions were maintained by artificial feeding (Ossi 2014), which has been shown to alter elk migration patterns including timing and decreased migration distances (Jones et al. 2014). In particular, roe deer feeding stations are often distributed at higher elevations in alpine regions, while they are commonly deployed at comparatively lower altitudes at the valley bottoms in Scandinavia (Mysterud 1999, Ramanzin et al. 2007). While winter severity has been suggested the main driver of migration in autumn (Nelson 1995), the availability, quality and predictability of forage most commonly explains ungulate migration from winter to summer ranges (Albon and Langvatn 1992, Hebblewhite et al. 2008, Mysterud et al. 2011)

Especially red deer migration probability was tied to seasonality and predictability of NDVI, consistent with hypotheses on seasonality of forage resources (Mueller et al. 2011). The FMH has been tested for elk migration in North America (Hebblewhite et al. 2008) and red deer migration in Norway (Bischof et al. 2012), where movements of deer coincided with forage green-up and delays in plant phenology at higher elevations. In our study, contingency (seasonality and its predictability) affected the daily probability of migration in time-to-event models in spring and autumn for red deer, and autumn for roe deer. This confirms the hypothesis that migration should occur more when predictability of the spatiotemporal variability is high (Mueller et al. 2011). Sabine et al. (2002) suggested that large variation in resources may drive plasticity in migration probability and timing. Concurrently, we showed that migration distance was positively associated with seasonality for red

deer. In general, deer that migrated farther initiated migration sooner, especially in more seasonal environments.

However, for roe deer we expected a stronger disconnect between covariates describing green-up and migration probability as well as timing. Being a smaller-bodied concentrate selector, roe deer may not need to undergo migration to access high quality forage (Mysterud et al. 2012), especially if heterogeneity can be provided at smaller spatial scales as in mountainous habitats (Gaudry et al. 2015). Our analysis of the daily probability of migration showed some evidence of the FMH being also applicable to roe deer (Peters et al. *in prep* [Chapter 2]). In spring, metrics of plant emergence, especially ΔNDVI were important predictors for the initiation of migration by both species. For roe deer the positive values of ΔNDVI increased the probability of departure from winter range, while the absolute NDVI value decreased departure probability. This suggests that for roe deer not the absolute value of NDVI is important, but rather the rate of change initiates spring migrations. Mule deer in North America followed similar patterns, where the probability of daily migration increased in response to the absolute and the daily change in NDVI (Monteith et al. 2011). Further, roe deer migrated sooner than red deer in spring, perhaps tracking forbs because of the delayed green-up of graminoids compared to forbs (Hebblewhite et al. 2008). Also, in spring much browse is located above snow cover and browse phenology may therefore not necessarily be as tightly linked to snow melt as graminoids (Mysterud et al. 2011).

In autumn high values of NDVI delayed migration in both species consistent with the hypothesis of taking advantage of delayed phenology at higher elevations (Albon and Langvatn 1992). Shrubs undergo a delayed green-up at higher elevations (Hebblewhite et

al. 2008), which may extend the time especially roe deer can access forage of higher protein content than they would find at lower elevations. Concurrently, roe deer remained on summer ranges longer than red deer, supporting the interpretation that autumn shrub phenology was driving roe deer autumn migration. Even small improvements in body condition during late autumn or early winter may substantially reduce winter mortality (Hobbs 1989). For example, mule deer in a mountainous study area delayed migration in autumn to take advantage of higher forage quality on summer ranges and avoid density-dependent competition on winter range although they risked encountering severe winter conditions (Monteith et al. 2011). Nicholson (1995) also found that mule deer spent as much times as possible on summer range, likely to avoid high competition on winter range. It has therefore been assumed that it is beneficial to minimize the amount of time deer spend on winter ranges (Sawyer et al. 2005). Overall our results support the hypothesis that forage and its phenology may not be the main driver for roe deer migration, but certainly should be considered as an important factor, especially for fall migration (Peters et al. *in prep*. [Chapter 2]).

For roe deer, migration probability decreased with increasing proportions of forests and high average NDVI values on winter ranges. We believe that both covariates, i.e. % forest and NDVI, indicate the same result, which is supported by their strong correlation (r=0.84). In general, NDVI can perform poorly in predicting understory forage dynamics when high amounts of conifer forests are present (Chen et al. 2004). We reason that the increased probability of migration with increasing forest cover and NDVI on roe deer winter ranges reflects that roe deer may be more migratory in forested mountainous landscapes compared to flat agricultural

landscapes. Roe deer began to colonize agricultural landscapes in the late seventies across Europe (Gaillard et al. 2013). These landscapes provide higher quality diets and roe deer inhabiting agricultural landscapes generally have higher body masses (Hewison et al. 2009). Although agriculture has been suggested to be major drivers of decreasing migration probabilities and distances in ungulates (Mysterud 2013, Wilmers and Levi 2013), it was highly correlated (r>0.70) with the stronger predictors % forest and NDVI based on univariate assessments and therefore was not included in our top models.

Migratory distance has previously been shown to be a function of body mass (Hain et al. 2012), consistent with our results. This may be because of metabolic or biomechanical constraints affecting the energetic cost of movement (Eisenberg 1981, Hein et al. 2012). However, there are many alternative competing hypotheses to explain our observations, including supplementary feeding (Jones et al. 2014) or landscape permeability (Cagnacci et al. 2011). Interestingly, we found marginal evidence for decreasing roe deer migration distances with increasing human activity (nightlights), consistent with many previous studies showing migration patterns may be impacted by anthropogenic development (Berger 2004, Lendrum et al. 2013, Seidler et al. 2015). In contrast, red deer migrated farther with increasing human activity on winter ranges. The daily probability of migration, however, was higher with increased human activity for both species. Lendrum et al. (2013) found that mule deer that migrated through less developed areas traveled at slower speeds and greater distances compared to deer that migrated through more developed areas. Our contrasting species-specific findings on the effects of human activity on migration

distance may reflect an overall difference in habitat availability between the two species or sensitivity to human disturbance. Interestingly, in contrast to other studies, including white-tailed deer (Nixon et al. 1991) and roe deer (Mysterud 1999) in which females migrated farther than males, we found no sex-related differences in migration distance for either species.

There is little consensus on differences in the probability of migration between sexes in ungulates. For example, in a study by Nicholson (1995) all male mule deer migrated, but only 50% of females, while Ferguson and Elkie (2004) found no sex-differences in migration propensity of caribou (*Rangifer tarandus caribou*). In our study the probability of migration was higher for male red deer, while we found no sex differences in the probability of migration for roe deer. This is in contrast to Mysterud (1999) who found that 70% of female roe deer, but only 38% of the males were migratory in a low-density population in south-eastern Norway. Our results of overall low migratory probability and sex-related differences in roe deer could be a function of density in this small territorial cervid (e.g., the competition avoidance hypothesis, Mysterud et al. 2011). Migration is energetically costly; especially for a smaller territorial species and the costs may not outweigh the benefits of migration (Peters et al. *in prep*. [Chapter 3]). Similarly, Eggeman et al. (*in revision*) suggested that elk switch in a facultative manner between resident and migratory behavior as a function of elk density on winter range, forage and predation risk. Unfortunately, we were unable to estimate density and thus, address its effects on the overall probability of migration and sex-related migratory differences. This could be a profitable avenue for future research.

Sex-specific differences in timing of migration are especially expected to arise due to the timing of breeding and parturition (Mysterud 1999, Ramanzin et al. 2007, Cagnacci et al. 2011, Jarnemo 2008). For example, the growing season is particularly important for females, because the forage quality that females consume during that period has been directly linked to offspring survival for roe deer (Gaillard et al. 1998) and red deer (Cook et al. 2013). Thus, females may be under pressure to synchronize migration dates with birth and peak protein levels of emergent vegetation (Loe et al. 2005), which is consistent with the more synchronized spring migration (smaller SDs in migration dates; Fig. 4-5) of female roe- and red deer compared to males. Nutritional demands of females in spring are highest due to gestation and lactation (Robbins and Robbins 1979). Thus, timing of spring migration may have important implications for juvenile birth weight and probability of survival (Lomas and Bender 2007). Being income breeders with high levels of resource allocation to reproduction, one would expect forage to be especially important during spring for female roe deer. Indeed maternal condition and climate during late gestation and lactation affects fawn survival in roe deer (Gaillard et al. 1997). We expected earlier spring and delayed autumn migrations for male roe deer. In general, we only found significant sex-specific differences in roe deer migration in autumn, consistent with Cagnacci et al. (2011). Roe deer migrated sooner than red deer in spring and later in autumn as expected under the competition avoidance hypothesis, confirming that forage may not be the main driver for migration in roe deer. Roe deer males should remain on their summer ranges as long as possible to maintain breeding opportunities (Cagnacci et al. 2011). Mysterud (1999) also found no difference in timing of spring

migration in roe deer. It is possible that roe deer try to spend as little time as possible on winter range to avoid density dependent effects (Mysterud et al. 2011).

Lastly, ongoing climate change is predicted to alter ecosystem structure and function (Walther et al. 2002) especially through the influence of climate change on phenology of plants and animals (Stenseth et al. 2002). Overall, we found that seasonality of vegetation affected the probability, the daily probability of migration as well as the migration distance, which is in agreement with the general hypothesis that migration arises to obtain access to seasonal forage resources in more predictable landscapes. Climate change has the potential to alter these relationships, especially through changes in the timing of spring and autumn phenology (Stenseth et al. 2002). Consequently, climate change may alter spring and autumn migration patterns and understanding which factors affect the initiation of migration is important when aiming to predict future changes. Plasticity in timing of migration may allow ungulates to partially compensate for trophic mismatched phenology between reproduction and plant phenology when reproduction traits are less plastic (Plard et al. 2014). Roe deer in particular show very low flexibility in the parturition dates due to their reproductive strategy of delayed implantation. Gaillard et al. (2013) showed that roe deer population dynamics were negatively affected by earlier onsets of spring. Overall, environmental alterations, including changing plant phenology under climate change will alter the benefits of seasonal migration for partially migratory ungulate populations (Middleton et al. 2013).

LITERATURE CITED

Albon, S. D. and R. Langvatn. 1992. Plant Phenology and the Benefits of Migration in a Temperate Ungulate. Oikos 65:502-513.

Andersen, P. and R. Gill. 1982. Cox's regression model for counting processes, a large sample study. Annals of Statistics 10:1100-1120.
Arnold, T. W. 2010. Uninformative Parameters and Model Selection Using Akaike's Information Criterion. Journal of Wildlife Management 74:1175-1178.
Ball, J. P., C. Nordengren, and K. Wallin. 2001. Partial migration by large ungulates: characteristics of seasonal moose Alces alces ranges in northern Sweden. Wildlife Biology 7:39-47.
Bauer, S. and B. J. Hoye. 2014. Migratory Animals Couple Biodiversity and Ecosystem Functioning Worldwide. Science 344.
Berbert, J. M. and W. F. Fagan. 2012. How the interplay between individual spatial memory and landscape persistence can generate population distribution patterns. Ecological Complexity 12:1-12.
Berger, J. 2004. The last mile: How to sustain long-distance migration in mammals. Conservation Biology 18:320-331.
Bischof, R., L. E. Loe, E. L. Meisingset, B. Zimmermann, B. Van Moorter, and A. Mysterud. 2012. A Migratory Northern Ungulate in the Pursuit of Spring: Jumping or Surfing the Green Wave? American Naturalist 180:407-424.
Bjorneraas, K., B. Van Moorter, C. M. Rolandsen, and I. Herfindal. 2010. Screening Global Positioning System Location Data for Errors Using Animal Movement Characteristics. Journal of Wildlife Management 74:1361-1366.
Bocci, A., A. Monaco, P. Brambilla, I. Angelini, and S. Lovari. 2010. Alternative Strategies of Space use of Female Red Deer in a Mountainous Habitat. Annales Zoologici Fennici 47:57-66.
Bolger, D. T., W. D. Newmark, T. A. Morrison, and D. F. Doak. 2008. The need for integrative approaches to understand and conserve migratory ungulates. Ecology Letters 11:63-77.
Bowyer, R. T. 2004. Sexual Segregation in Ruminants: Definitions, Hypotheses, and Implications for Conservation and Management.
Bowyer, R. T. and J. G. Kie. 2006. Effects of scale on interpreting life-history characteristics of ungulates and carnivores. Diversity and Distributions 12:244-257.
Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281-300.
Bunnefeld, N., L. Boerger, B. van Moorter, C. M. Rolandsen, H. Dettki, E. J. Solberg, and G. Ericsson. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. Journal of Animal Ecology 80:466-476.
Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, USA.
Burrill, A. and P. Vossen. 1992. Development of an operational agro-meteorological monitoring system. In: F. Toselli, J. Meyer-Roux (eds). Proceedings of conference on the application of remote sensing to agricultural statistics, 26-27 November 1991, Belgirate, Italy. EUR 14262 EN, Office for Official Publications of the EU, Luxembourg, p 357-360.
Cagnacci, F., S. Focardi, A. Ghisla, B. Van Moorter, E. Gurarie, M. Heurich, A. Mysterud, J. Linnell, M. Panzacchi, and M. Roel. in revision. How many routes

lead to migration? Re-establishing the link between definitions, methods and movemet ecology. Journal of Animal Ecology.
Cagnacci, F., S. Focardi, M. Heurich, A. Stache, A. J. M. Hewison, N. Morellet, P. Kjellander, J. D. C. Linnell, A. Mysterud, M. Neteler, L. Delucchi, F. Ossi, and F. Urbano. 2011. Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. Oikos 120:1790-1802.
Chapman, B. B., C. Brönmark, J.-Å. Nilsson, and L.-A. Hansson. 2011. The ecology and evolution of partial migration. Oikos 120:1764-1775.
Cleves, M. A., W. W. Gould, and R. G. Gutierrez. 2002. An Introduction to Survival Analaysis using STATA. Stata Press, STATA Corporation College Station, TX, USA.
Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red Deer: Behaviour and Ecology of Two Sexes, Chicago.
Colwell, R. K. 1974. Predictability, Constancy, and Contingency of Periodic Phenomena. Ecology 55:1148-1153.
Cook, R. C., J. G. Cook, D. J. Vales, B. K. Johnson, S. M. McCorquodale, L. A. Shipley, R. A. Riggs, L. L. Irwin, S. L. Murphie, B. L. Murphie, K. A. Schoenecker, F. Geyer, P. B. Hall, R. D. Spencer, D. A. Immell, D. H. Jackson, B. L. Tiller, P. J. Miller, and L. Schmitz. 2013. Regional and seasonal patterns of nutritional condition and reproduction in elk. Wildlife Monographs 184:1-45.
Cox, D. T. C. 1972. Regression Models and Life Tables (with Discussion). Journal of the Royal Statistical Society B 74:187-220.
Debeffe, L., S. Focardi, C. Bonenfant, A. J. M. Hewison, N. Morellet, C. Vanpé, M. Heurich, P. Kjellander, J. C. Linnell, A. Mysterud, M. Pellerin, P. Sustr, F. Urbano, and F. Cagnacci. 2014. A one night stand? Reproductive excursions of female roe deer as a breeding dispersal tactic. Oecologia 176:431-443.
Dingle, H. 2006. Animal migration: is there a common migratory syndrome? Journal of Ornithology 147:212-220.
Dussault, C., J. P. Ouellet, R. Courtois, J. Huot, L. Breton, and J. Larochelle. 2004. Behavioural responses of moose to thermal conditions in the boreal forest. Ecoscience 11:321-328.
Eggeman, S., M. Hebblewhite, H. Bohm, J. Whittington, and E. Merrill. *in review*. Behavioral Flexibility in Migratory Behavior in a Long-Lived Large Herbivore. Journal of Animal Ecology.
Eisenberg, F. 1983. The Mammalian Radiations: An Analysis of Trends in Evolution, Adaptation, and Behavior. University of Chicago Press, Chicago.
Elton, C. 1927. Animal Ecology. Sidgwick and Jackson, London.
English, A. K., A. L. Chauvenet, K. Safi, and N. Pettorelli. 2012. Reassessing the determinants of breeding synchrony in ungulates. Plos One 7:e41444.
Fieberg, J., D. W. Kuehn, and G. D. DelGiudice. 2008. Understanding Variation in Autumn Migration of Northern White-Tailed Deer by Long-Term Study.
Frair, J. L., J. Fieberg, M. Hebblewhite, F. Cagnacci, N. J. DeCesare, and L. Pedrotti. 2010. Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2187-2200.

Fryxell, J. M. 1991. Forage Quality and Aggregation by Large Herbivores. American Naturalist 138:478-498.
Fryxell, J. M., M. Hazell, L. Börger, B. D. Dalziel, D. T. Haydon, J. M. Morales, T. McIntosh, and R. C. Rosatte. 2008. Multiple movement modes by large herbivores at multiple spatiotemporal scales. Proceedings of the National Academy of Sciences 105:19114-19119.
Fryxell, J. M. and A. R. E. Sinclair. 1988. Causes and Consequences of Migration by Large Herbivores. Trends in Ecology & Evolution 3:237-241.
Gaillard, J.-M., J.-M. Boutin, D. Delorme, G. V. Laere, P. Duncan, and J.-D. Lebreton. 1997. Early Survival in Roe Deer: Causes and Consequences of Cohort Variation in Two Contrasted Populations. Oecologia 112:502-513.
Gaillard, J.-M., A. J. Mark Hewison, F. Klein, F. Plard, M. Douhard, R. Davison, and C. Bonenfant. 2013. How does climate change influence demographic processes of widespread species? Lessons from the comparative analysis of contrasted populations of roe deer. Ecology Letters 16:48-57.
Gaillard, J. M., R. Andersen, D. Delorme, and J. D. C. Linnell. 1998. Family effects on growth and survival of juvenile roe deer. Ecology 79:2878-2889.
Gaudry, W., S. Saïd, J.-M. Gaillard, T. Chevrier, A. Loison, D. Maillard, and C. Bonenfant. 2015. Partial migration or just habitat selection? Seasonal movements of roe deer in an Alpine population.
Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. Statistics in Medicine 27:2865-2873.
Gillies, C., M. Hebblewhite, S. E. Nielsen, M. Krawchuk, C. Aldridge, J. Frair, C. Stevens, D. J. Saher, and C. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887-898.
Gordon, I. J., A. J. Hester, and M. Festa-Bianchet. 2004. REVIEW: The management of wild large herbivores to meet economic, conservation and environmental objectives. Journal of Applied Ecology 41:1021-1031.
Grovenburg, T. W., C. N. Jacques, R. W. Klaver, C. S. DePerno, T. J. Brinkman, C. C. Swanson, and J. A. Jenks. 2011. Influence of landscape characteristics on migration strategies of white-tailed deer. Journal of Mammalogy 92:534-543.
Hall, D. K., G. A. Riggs, and V. V. Salomonson. 2000. MODIS/Terra snow cover 8-day L3. Global 500m Grid V03, February 2000 to February 2002. National Snow and Ice Data Center. Digital media. , Boulder, CO, USA.
Hamel, S., J. M. Gaillard, N. G. Yoccoz, A. Loison, C. Bonenfant, and S. Descamps. 2010. Fitness costs of reproduction depend on life speed: empirical evidence from mammalian populations. Ecology Letters 13:915-935.
Hamel, S., M. Garel, M. Festa-Bianchet, J. M. Gaillard, and S. D. Cote. 2009. Spring Normalized Difference Vegetation Index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. Journal of Applied Ecology 46:582-589.
Hansen, M. C., P. V. Potapov, R. Moore, M. Hancher, S. A. Turubanova, A. Tyukavina, D. Thau, S. V. Stehman, S. J. Goetz, T. R. Loveland, A. Kommareddy, A. Egorov, L. Chini, C. O. Justice, and J. R. G. Townshend. 2013. High-Resolution Global Maps of 21st-Century Forest Cover Change. Science 342:850-853.

Hastie, T. J. and R. Tibshirani. 1990. Generalized additive models. Chapman and Hall, London.
Hebblewhite, M., E. H. Merrill, and G. McDermid. 2008. A mutli-scale test of the forage maturation hypothesis for a partially migratory montane elk population. Ecological Monographs 78:141-166.
Hein, A. M., C. Hou, and J. F. Gillooly. 2012. Energetic and biomechanical constraints on animal migration distance. Ecology Letters 15:105-110.
Hewison, A. J. M., N. Morellet, H. Verheyden, T. Daufresne, J.-M. Angibault, B. Cargnelutti, J. Merlet, D. Picot, J.-L. Rames, J. Joachim, B. Lourtet, E. Serrano, E. Bideau, and N. Cebe. 2009. Landscape fragmentation influences winter body mass of roe deer. Ecography 32:1062-1070.
Hobbs, N. T. 1989. Linking Energy Balance to Survival in Mule Deer: Development and Test of a Simulation Model. Wildlife Monographs:3-39.
Hobbs, N. T. 1996. Modification of Ecosystems by Ungulates. The Journal of Wildlife Management 60:695-713.
Hofmann, R. R. 1989. Evolutionary Steps of Ecophysiological Adaptation and Diversification of Ruminants - a Comparative View of Their Digestive-System. Oecologia 78:443-457.
Hopcraft, J. G. C., J. M. Morales, H. L. Beyer, M. Borner, E. Mwangomo, A. R. E. Sinclair, H. Olff, and D. T. Haydon. 2014. Competition, predation, and migration: individual choice patterns of Serengeti migrants captured by hierarchical models. Ecological Monographs 84:355-372.
Hosmer, D. W. and S. Lemeshow, editors. 2000. Applied Logistic Regression. John Wiley and Sons, New York, USA.
Hosmer, D. W., S. Lemeshow, and S. May. 2008. Applied Survival Analysis. Regression Modeling of Time-to-Event Data. John Wiley & Sons, Hoboke, NJ.
Jarnemo, A. 2008. Seasonal migration of male red deer (Cervus elaphus) in southern Sweden and consequences for management. European Journal of Wildlife Research 54:327-333.
Jones, J. D., M. J. Kauffman, K. L. Monteith, B. M. Scurlock, S. E. Albeke, and P. C. Cross. 2014. Supplemental feeding alters migration of a temperate ungulate. Ecological Applications 24:1769-1779.
Jonzén, N., E. Knudsen, R. Holt, and B. Sæther. 2011. Uncertainty and predictability: the niches of migrants and nomads.*in* E. J. Milner-Gulland, J. Fryxell, and A. R. E. Sinclair, editors. Animal Migration: A Synthesis. Oxford University Press, Oxford.
Kaitala, A., V. Kaitala, and P. Lundberg. 1993. A Theory of Partial Migration. American Naturalist 142:59-81.
Ketterson, E. D. and V. Nolan. 1976. Geographic Variation and Its Climatic Correlates in the Sex Ratio of Eastern-Wintering Dark-Eyed Juncos (Junco Hyemalis Hyemalis). Ecology 57:679-693.
Kie, J. G. and R. T. Bowyer. 1999. Sexual Segregation in White-Tailed Deer: Density-Dependent Changes in Use of Space, Habitat Selection, and Dietary Niche. Journal of Mammalogy 80:1004-1020.
Kleiber, C. and A. Zeileis. 2008. Applied Econometrics with R. Springer-Verlag, New York.

Lendrum, P. E., C. R. Anderson, Jr., K. L. Monteith, J. A. Jenks, and R. T. Bowyer. 2013. Migrating Mule Deer: Effects of Anthropogenically Altered Landscapes. Plos One 8:e64548.

Levey, D. J. and F. G. Stiles. 1992. Evolutionary Precursors of Long-Distance Migration: Resource Availability and Movement Patterns in Neotropical Landbirds. The American Naturalist 140:447-476.

Loe, L. E., C. Bonenfant, A. Mysterud, J. M. Gaillard, R. Langvatn, F. Klein, C. Calenge, T. Ergon, N. Pettorelli, and N. C. Stenseth. 2005. Climate predictability and breeding phenology in red deer: timing and synchrony of rutting and calving in Norway and France. Journal of Animal Ecology 74:579-588.

Loison, A., M. Festa-Bianchet, J. M. Gaillard, J. T. Jorgenson, and J. M. Jullien. 1999. Age-specific survival in five populations of ungulates: Evidence of senescence. Ecology 80:2539-2554.

Lomas, L. A. and L. C. Bender. 2007. Survival and Cause-Specific Mortality of Neonatal Mule Deer Fawns, North-Central New Mexico. Journal of Wildlife Management 71:884-894.

Lone, K., L. E. Loe, T. Gobakken, J. D. C. Linnell, J. Odden, J. Remmen, and A. Mysterud. 2014. Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. Oikos 123:641-651.

Lone, K., L. E. Loe, E. L. Meisingset, I. Stamnes, and A. Mysterud. 2015. An adaptive behavioural response to hunting: surviving male red deer shift habitat at the onset of the hunting season. Animal Behaviour 102:127-138.

Middleton, A. D., M. J. Kauffman, D. E. McWhirter, J. G. Cook, R. C. Cook, A. A. Nelson, M. D. Jimenez, and R. W. Klaver. 2013. Animal migration amid shifting patterns of phenology and predation: Lessons from a Yellowstone elk herd. Ecology.

Mitchell-Jones, A., G. Amori, W. Bogdanowicz, B. Kryštufek, P. J. H. Reijnders, F. Spitzenberger, M. Stubbe, J. B. M. Thissen, V. Vohralik, and J. Zima. 1999. The atlas of European mammals. T & AD Poyser, London.

Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, R. W. Klaver, and R. T. Bowyer. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. Ecosphere 2:art47.

Morellet, N., C. Bonenfant, L. Börger, F. Ossi, F. Cagnacci, M. Heurich, P. Kjellander, J. D. C. Linnell, S. Nicoloso, P. Sustr, F. Urbano, and A. Mysterud. 2013. Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. Journal of Animal Ecology 82:1326-1339.

Moyes, K., T. Coulson, B. J. T. Morgan, A. Donald, S. J. Morris, and T. H. Clutton-Brock. 2006. Cumulative reproduction and survival costs in female red deer. Oikos 115:241-252.

Mueller, T. and W. F. Fagan. 2008. Search and navigation in dynamic environments – from individual behaviors to population distributions. Oikos 117:654-664.

Mueller, T., K. A. Olson, G. Dressler, P. Leimgruber, T. K. Fuller, C. Nicolson, A. J. Novaro, M. J. Bolgeri, D. Wattles, S. DeStefano, J. M. Calabrese, and W. F. Fagan. 2011. How landscape dynamics link individual- to population-level

movement patterns: a multispecies comparison of ungulate relocation data. Global Ecology and Biogeography 20:683-694.
Mysterud, A. 1999. Seasonal migration pattern and home range of roe deer (Capreolus capreolus) in an altitudinal gradient in southern Norway. Journal of Zoology 247:479-486.
Mysterud, A. 2013. Ungulate migration, plant phenology, and large carnivores: The times they are a-changin'. Ecology 94:1257-1261.
Mysterud, A., R. Bischof, L. E. Loe, J. Odden, and J. Linnell. 2012. Contrasting migration tendencies of sympatric red deer and roe deer suggest multiple causes of migration in ungulates. Ecosphere 3:10, art92.
Mysterud, A., R. Langvatn, N. G. Yoccoz, and N. C. Stenseth. 2001. Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. Journal of Animal Ecology 70:915-923.
Mysterud, A., L. E. Loe, B. Zimmermann, R. Bischof, V. Veiberg, and E. Meisingset. 2011. Partial migration in expanding red deer populations at northern latitudes - a role for density dependence? Oikos 120:1817-1825.
Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. Biometrika 78:691-692.
Nelson, M. E. 1995. Winter range arrival and departure of white-tailed deer in northeastern Minnesota. Canadian Journal of Zoology 73:1069-1076.
Nelson, M. E. 1998. Development of migratory behavior in northern white- tailed deer. Canadian Journal of Zoology 76:426-432.
Nicholson, M. C., R. T. Bowyer, and J. G. Kie. 1997. Habitat selection and survival of mule deer: Tradeoffs associated with migration. Journal of Mammalogy 78:483-504.
Nielsen, J. K., P. N. Hooge, S. J. Taggart, and A. C. Seitz. 2014. Characterizing Pacific halibut movement and habitat in a Marine Protected Area using net squared displacement analysis methods. Marine Ecology Progress Series 517:229-250.
Nussey, D. H., D. W. Coltman, T. Coulson, L. E. B. Kruuk, A. Donald, S. J. Morris, T. H. Clutton-Brocks, and J. Pemberton. 2005. Rapidly declining fine-scale spatial genetic structure in female red deer. Molecular Ecology 14:3395-3405.
Ossi, F. 2014. Ecological determinants of roe deer (Capreolus capreolus) spatial behavior and movement in limiting conditions. Université Claude Bernard – Lyon 1, Lyon, France.
Ossi, F., J. M. Gaillard, M. Hebblewhite, and F. Cagnacci. 2015. Snow sinking depth and forest canopy drive winter resource selection more than supplemental feeding in an alpine population of roe deer. European Journal of Wildlife Research 61.
Owensmith, N. and P. Novellie. 1982. What Should a Clever Ungulate Eat. American Naturalist 119:151-178.
Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk Journal of Wildlife Management 48:474-488.
Pettorelli, N., J. O. Vik, A. Mysterud, J. M. Gaillard, C. J. Tucker, and N. C. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology & Evolution 20:503-510.

Plard, F., J.-M. Gaillard, T. Coulson, A. J. M. Hewison, D. Delorme, C. Warnant, and C. Bonenfant. 2014. Mismatch Between Birth Date and Vegetation Phenology Slows the Demography of Roe Deer. PLoS Biol 12:e1001828.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival Analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7-15.

QGIS Development Team. 2014. QGIS Geographic Information System. . Open Source Geospatial Foundation Project.

R Development Core Team. 2013. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. .

Ramanzin, M., E. Sturaro, and D. Zanon. 2007. Seasonal migration and home range of roe deer (Capreolus capreolus) in the Italian eastern Alps. Canadian Journal of Zoology-Revue Canadienne De Zoologie 85:280-289.

Robbins, C. T. and B. L. Robbins. 1979. Fetal and Neonatal Growth Patterns and Maternal Reproductive Effort in Ungulates and Subungulates. The American Naturalist 114:101-116.

Sabine, D. L., S. F. Morrison, H. A. Whitlaw, W. B. Ballard, G. J. Forbes, and J. Bowman. 2002. Migration behavior of white-tailed deer under varying winter climate regimes in New Brunswick. Journal of Wildlife Management 66:718-728.

Sawyer, H. and M. J. Kauffman. 2011. Stopover ecology of a migratory ungulate. Journal of Animal Ecology 80:1078-1087.

Sawyer, H., F. Lindzey, and D. McWhirter. 2005. Mule Deer and Pronghorn Migration in Western Wyoming. Wildlife Society Bulletin (1973-2006) 33:1266-1273.

Seidler, R. G., R. A. Long, J. Berger, S. Bergen, and J. P. Beckmann. 2015. Identifying impediments to long-distance mammal migrations. Conservation Biology 29:99-109.

Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. Bioscience 37:789-795 & 798-799.

Singh, N. J., L. Borger, H. Dettki, N. Bunnefeld, and G. Ercsson. 2012. From migration to nomadism: movemnet varaibility in a northern ungulate accross its latitudinal range. Ecological Applications 22:2007-2020.

Skov, C., H. Baktoft, J. Brodersen, C. Bronmark, B. Chapman, L. A. Hansson, and P. A. Nilsson. 2011. Sizing up your enemy: individual predation vulnerability predicts migratory probability. Proceedings of the Royal Society B-Biological Sciences 278:1414-1418.

Small, C., F. Pozzi, and C. D. Elvidge. 2005. Spatial analysis of global urban extent from DMSP-OLS night lights. Remote Sensing of Environment 96:277-291.

Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K. S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. Science 297:1292-1296.

Stopher, K. V., D. H. Nussey, T. H. Clutton-Brock, F. Guinness, A. Morris, and J. M. Pemberton. 2011. The red deer rut revisited: female excursions but no evidence females move to mate with preferred males. Behavioral Ecology.

Teitelbaum, C. S., W. F. Fagan, C. H. Fleming, G. Dressler, J. M. Calabrese, P. Leimgruber, and T. Mueller. 2015. How far to go? Determinants of migration distance in land mammals. Ecology Letters 18:545-552.

Therneau, T. 2015. A Package for Survival Analysis in S. version 2.38.
Therneau, T. and P. Grambsch. 2000. Modeling Survival Data: Extending the Cox Model. Springer Verlag.
Vanpe, C., N. Morellet, P. Kjellander, M. Goulard, O. Liberg, and A. J. M. Hewison. 2009. Access to mates in a territorial ungulate is determined by the size of a male's territory, but not by its habitat quality. Journal of Animal Ecology 78:42-51.
Venables, W. N. and B. D. Ripley. 2002. Modern Applied Statistics with S. Fourth edition. Springer.
Verheyden, H., L. Aubry, J. Merlet, P. Petibon, B. Chauveau-Duriot, N. Guillon, and P. Duncan. 2011. Faecal nitrogen, an index of diet quality in roe deer Capreolus capreolus? Wildlife Biology 17:166-175.
Vuolo, F., M. Mattiuzzi, A. Klisch, and C. Atzberger. 2012. Data service platform for MODIS Vegetation Indices time series processing at BOKU Vienna: current status and future perspectives. Pages 85380A-85380A-85310.
Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389-395.
Wilmers, C. C. and T. Levi. 2013. Do irrigation and predator control reduce the productivity of migratory ungulate herds? Ecology 94:1264-1270.
Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed Effects Models and Extensions in Ecology with R. 1st Edition., 2009, XXII, 574 p.
Zweifel-Schielly, B., Y. Leuenberger, M. Kreuzer, and W. Suter. 2012. A herbivore's food landscape: seasonal dynamics and nutritional implications of diet selection by a red deer population in contrasting Alpine habitats. Journal of Zoology 286:68-80.

Table 4-1. Predicted differences between partially migratory roe deer (*Capreolus capreolus*; 10 populations; N= 273) and red deer (*Cervus elaphus*; 12 populations; N=264) for the overall frequency (i.e. probability), distance and timing of migration. Study areas of both species ranged across similar latitudinal gradients in Europe and animal location data were collected between 1999 and 2014.

	Between Species	**Between Sexes**	**Between Population**	
			Topographic complexity & latitude	**Resources (e.g. NDVI, snow, predictability)**
FREQUNCY	**P_{F1}:** Under the forage maturation hypothesis, higher proportion of migrants in red deer populations.	**P_{F2}**: No differences in migration frequency between roe-deer males and females due to low sexual dimorphism.	**P_{F3}**: Higher proportion of migrants with increasing *topographic complexity* and *latitude, winter severity, predictability of forage.*	
DISTANCE		**P_{D1}**: Red migrate further because of body size	**P_{D2}**: Migration distance increases with latitude and decreases with topographic complexity.	
TIMING	**$P_{T1.1}$:** Red deer migration synchronized with green-up and senescence more than roe deer (later in spring, earlier in autumn). **$P_{T1.2}$**: Roe deer autumn migration is more driven by winter weather and red deer autumn migration by forage senescence.	**P_{T2}:** Roe deer males migrate first in spring and last in autumn (i.e. after roe deer females and red deer) to establish and maintain territories for maximum duration.	**P_{T3}**: Delayed spring and earlier autumn migration at northern latitudes.	**P_{T4}**: Spring migration correlates with forage green-up and autumn migration correlates with onset of winter.

Table 4-2. The top logistic regression models within 2 units of the Akaike Information Criterion for small sample sizes (AICc) of the top ranked model approximating the probability of migration in a) roe deer (*Capreolus capreolus*) and b) red deer (*Cervus elaphus*) and the null model. Migration probability was estimated as a function of landscape, risk and vegetation predictor variables for 10 roe deer (N=273) and 12 red deer (N=264) study sites across Europe. Study area was included as random effect in generalized linear mixed models (GLMM). The adjusted R^2 (R^2_{Adj}), the number of parameters (K), the log likelihood (logLik), the AICc and the delta AICc (ΔAICc) are provided. Global positioning system (GPS) collar data were collected between 1999 and 2014).

Model	**R^2_{Adj}**	**K**	**logLik**	**AICc**	**ΔAICc**
Roe deer					
snow * slope + average NDVI	0.22	5	-114.71	239.7	0
snow * slope + % forest	0.21	5	-115.13	241.5	1.8
snow * slope + average NDVI + (1| study area)	0.22	6	-114.71	241.7	2
Null	/	1	-135.22	272.5	32.8
Red deer					
snow * slope + night lights + sex + (1| study area)	0.46	7	-126.26	267	0
snow * slope + night lights + sex	0.42	6	-132.39	278	11
Null	/	1	-182.38	366.8	99.8

Table 4-3. Model parameters (beta coefficients (β), standard errors (SE), Wald's z-values (z) and p-values (p)) of top two logistic regression model models describing the probability of migration for 10 roe deer (*Capreolus capreolus,* N = 273) and 12 red deer (*Cervus elaphus,* N = 264) study sites across Europe. A random intercept did not improve model fit for roe deer, but was included in the red deer model (GLMM). GPS collar data were collected between 1999 and 2014. All variables are standardized.

	No. 1 Model				**No. 2 Model**			
	β	***SE***	**z**	***p***	**β**	***SE***	**z**	***p***
Roe deer								
snow*slope	-1.34	0.68	-1.93	0.053	-1.23	0.69	-1.78	0.075
slope	0.87	0.32	2.72	0.007	0.90	0.32	2.79	0.005
average snow	1.14	0.42	2.78	0.005	1.27	0.41	3.09	0.002
NDVI	1.39	0.53	2.59	0.009	/	/	/	/
% forest	/	/	/	/	0.94	0.38	2.46	0.014
Intercept	-1.64	0.20	-7.95	<0.001	-1.60	0.20	-8.18	<0.001
Red deer								
snow*slope	-5.3	1.30	-4.21	<0.001				
average snow	2.46	0.80	2.9	0.004				
slope	1.04	0.70	1.59	0.111				
nightlights	1.86	0.60	3.08	0.002				
sex - male	1.49	0.40	3.33	<0.001				

Table 4-3 continued

Intercept	0.47	0.50	0.96	0.339
Random Intercept	Var = 1.18; SD=1.09			

Table 4-4. The best approximating negative binomial models (i.e. within 2 AIC_c units of the top ranked model) predicting migration distance (m) as a function of various landscape-, risk- and vegetation predictor variables in a) roe deer (*Capreolus capreolus*, 10 populations, N = 51) and b) red deer (*Cervus elaphus*,12 populations, N = 141) and the null model. We report the number of parameters (K), the log Likelihood (logLik), the Akaike Information Criterion for small sample sizes (AICc) and the delta AICc (ΔAICc). GPS collar data were collected between 1999 and 2014 across Europe.

Model	**K**	**logLik**	**AIC_c**	**ΔAIC_c**
Roe Deer				
Slope + nightlights	4	-506.87	1020.2	0
Null	2	-512.04	1028.3	8.09
Red Deer				
nightlights + latitude + contingency	5	-1416.6	2843.6	0
nightlights + latitude + % canopy closure + SD temperature	6	-1415.7	2844.1	0.49
Null	2	-1451.2	2906.5	62.92

Table 4-5. Model parameters (beta coefficients (β), standard errors (SE), t-values (t) and p-values (p)) of the best approximating negative binomial models (i.e. within 2 AIC_c of the top ranked model) describing migration distance for a) roe deer (*Capreolus capreolus,* N = 51, 10 populations) and b) red deer (*Cervus elaphus*, N = 141,12 populations). All variables are standardized. Populations spanned a similar latitudinal gradient across Europe. GPS collar data were collected between 1999 and 2014.

	No. 1 Model				**No. 2 Model**			
	β	***SE***	**t**	***p***	**β**	***SE***	**t**	***p***
Roe deer								
Slope	0.71	0.41	1.95	0.05				
Night lights	-0.69	0.37	-1.69	0.09				
Intercept	8.44	0.21	40.56	<0.001				
Theta		2.091 (SE=0.234)						
Red deer								
Latitude	0.6	0.13	4.62	<0.001	0.60	0.14	4.27	<0.001
Canopy closure	-0.34	0.14	-2.35	0.019	/	/	/	/
SD Temperature	0.35	0.13	2.73	0.006	/	/	/	/
Nightlights	0.37	0.14	2.67	0.008	0.46	0.12	3.72	<0.001
Contingency	/	/	/	/	0.40	0.14	2.78	0.005
Intercept	9.09	0.19	46.95	<0.001	9.32	0.2	45.82	<0.001
Theta		2.091 (SE=0.234)				2.069 (SE =0.231)		

Table 4- 6. The best approximating time-to-event models (i.e. within 2 AIC_c of the top ranked model) of the daily probability of migration as a function of various landscape, risk and vegetation predictor variables for a) roe deer (*Capreolus capreolus*, N=273, 10 populations) and b) red deer (*Cervus elaphus*, N=264, 12 populations) for spring and autumn and the null model. GPS collar data were collected between 1999 and 2014. A frailty term for study area did not improve model fit for roe deer, but was included in both red deer models. All variables are standardized.

Model	**K**	**LogLik**	**AIC_c**	**Δ AIC_c**
Roe Deer Spring Migration				
NDVI^{*1} + Δ NDVI^{*1} + %canopy closure + slope	4	-228.50	465	0
NDVI^{*1} + Δ NDVI^{*1} + %canopy closure + elevation + nightlights	5	-228.18	466.4	1.37
Null	0	-252.38	504.7	41.45
Roe Deer Autumn Migration				
NDVI^{*1} + contingency	2	-193.10	390.2	0
NDVI^{*1} + contingency + sex	3	-192.66	391.3	1.11
Null	0	-209.18	418.4	28.16
Red Deer Spring Migration				
Contingency + Δ NDVI^{*1} + sex + snow^{*1} + *frailty (study ID)*	5	-656.05	1320.1	0
Contingency + Δ NDVI^{*1} + sex + % snow^{*1}	4	-698.04	1400.1	80
Null	0	-716.87	1435.7	1115.6

Table 4-6 continued

Red Deer Autumn Migration				
Constancy + NDVI + sex + *frailty (study ID)*	4	-720.84	1447.7	0
Constancy + NDVI + sex	3	-754.61	1528.2	75.4
Null	0	-782.54	1565.1	113.4

Table 4-7. Hazard ratios (HR), p-values (p) and 95% CI of the top models describing the daily probability of spring and fall migration of a) roe deer (*Capreolus capreolus*, N = 273, 10 populations) and b) red deer (*Cervus elaphus*, N = 264, 12 populations) across Europe. See Table 4-6 for descriptions of the models. As the daily probability of migration increases, the probability of residency decreases in such that the hazard ratio > 1.0 means a lower probability of residency and a higher probability of migration. GPS collar data were collected between 1999 and 2014. All variables are standardized.

	No. 1 Model			**No. 2 Model**		
	HR	***p***	**95% CI**	**HR**	***p***	**95% CI**
Roe deer spring						
NDVI[*1]	0.27	0.004	(0.12-0.66)	0.35	0.025	(0.14-0.87
Δ NDVI[*1]	2.31	0.008	(1.25-4.27)	1.95	0.043	(1.02-3.73)
% canopy cover	2.63	0.005	(1.33-5.17)	2.42	0.015	(1.19-4.93)
Slope	2.28	<0.001	(1.46-3.55)	/	/	/
nightlights	/	/	/	1.8	0.007	(1.17-2.77)
elevation	/	/	/	2.51	0.004	(1.34-4.69)
Roe deer autumn						
NDVI[*1]	0.28	0.004	(0.12-0.66)	0.26	0.003	(0.11-0.63)
contingency	1.82	0.076	(0.94-3.51)	1.62	0.15	(0.84-3.14)
sex - male	/	/	/	0.66	0.17	(0.36-1.21)
Red deer spring						
Δ NDVI[*1]	1.25	0.066	(0.47-1.03)	/	/	/
Contingency	1.806	0.002	(1.24-2.61)	/	/	/

Table 4-7 continued

snow modis[*1]	0.632	0.16	(0.03-1.20)	/	/	/
sex - male	1.52	0.061	(0.98-2.36)	/	/	/
frailty (study ID)		<0.001		/	/	/
Red deer autumn						
NDVI*1	0.401	<0.001	(0.27-0.60)	/	/	/
Constancy	0.85	0.054	(0.53-1.36)	/	/	/
sex - male	2.37	<0.001	(1.57-3.57)			
frailty (study ID)		<0.001		/	/	/

[*1] Time-varying covariates

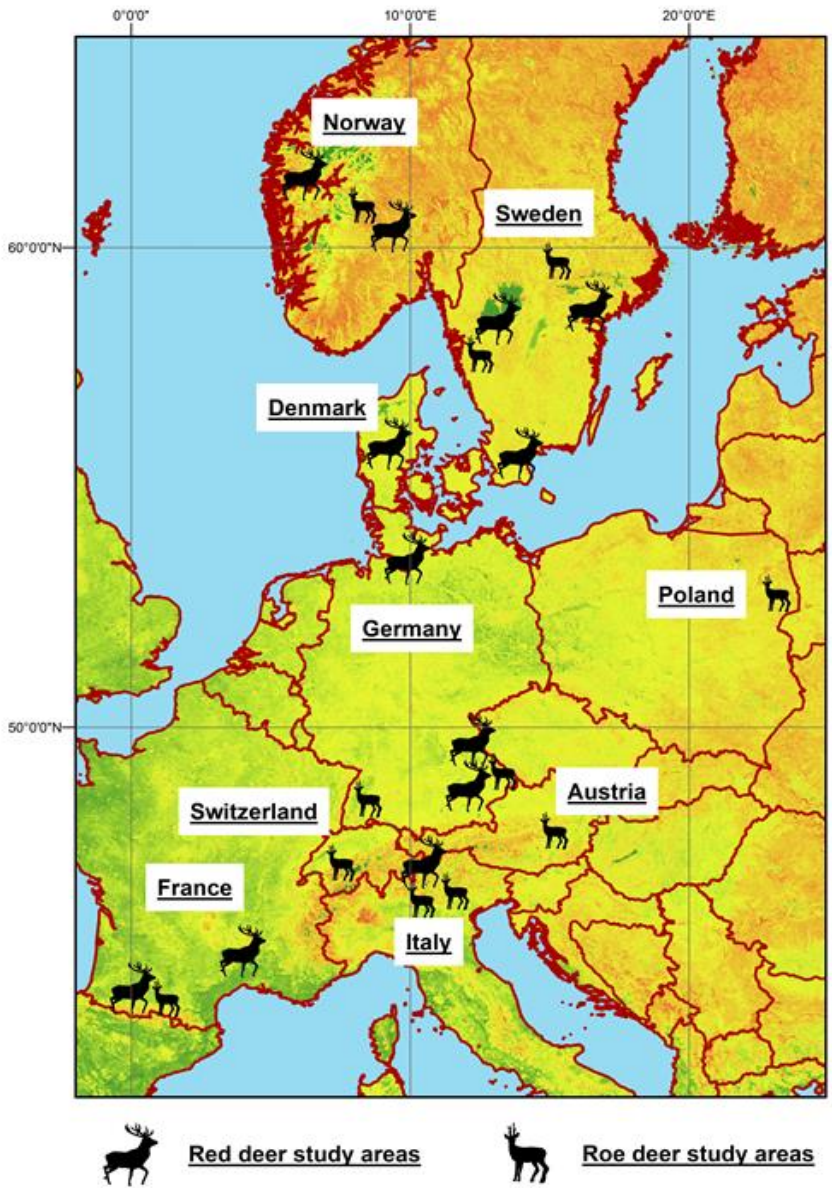


Figure 4-1. Roe deer (*Capreolus capreolus*, N = 273, 10 populations) and red deer (*Cervus elaphus*, N=264, 12 populations) study area locations. The spatial contingency (seasonality) layer is in the background, where red shades indicate high seasonality and green shades indicate low seasonality. GPS collar data were collected between 1999 and 2014.

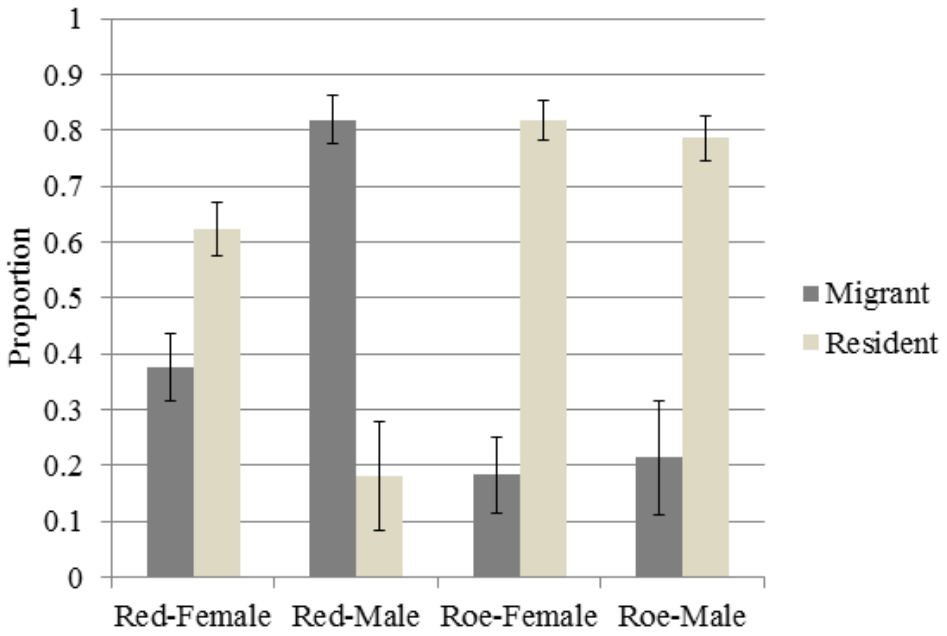


Figure 4-2. Comparison of the proportion (with SE) of migrant and resident individual roe deer (*Capreolus capreolus*, N = 273, 10 populations) and red deer (*Cervus elaphus*, N=264, 12 populations) by sex. Populations of both species spanned a similar latitudinal gradient across Europe from southern Italy to Norway, sampling years were 1999-2014.

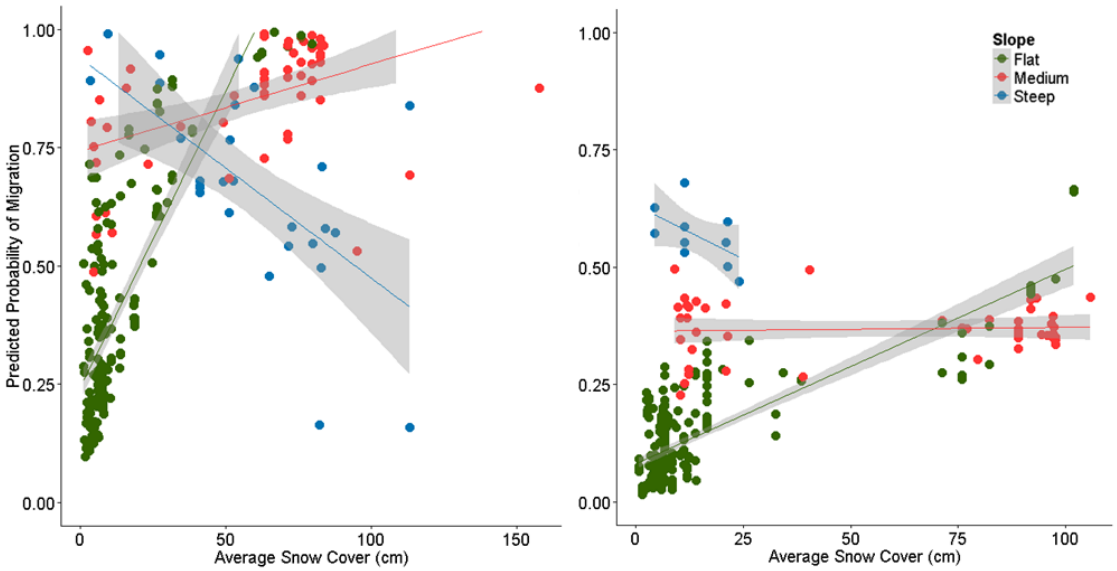


Figure 4-3. Predicted probability migration from top logistic regression models for red deer (*Cervus elaphus*; left) and roe deer (*Capreolus capreolus*; right) against the average snow cover by slope (with 95%CI). Slope classes range from flat = 0-12.7 degrees, medium = 12.8-24.3 degrees and steep= 24.4-36.1 degrees. GPS data collected between 1999 and 2014 from 10 roe- (N = 273) deer and 12 red (N = 264) deer study areas across Europe were to build logistic regression models.

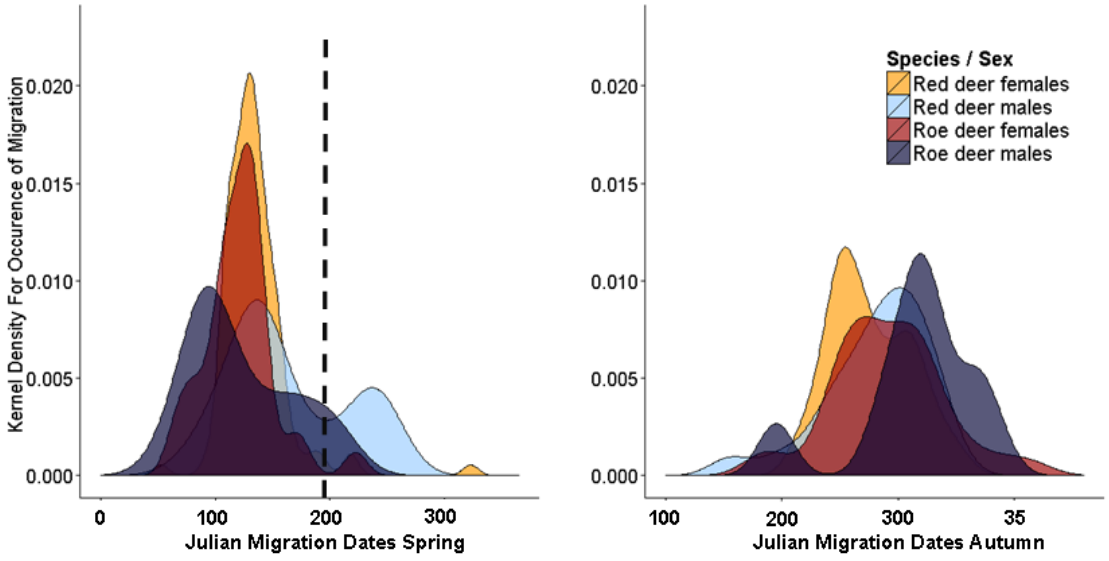


Figure 4-4. Kernel density plot of spring and autumn migration dates for red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) by sex. The black dotted line in the spring plot indicates the cut-off (July 15th) after which we excluded migration data in our analysis of migration probability, distance and timing (see text for details; N_{roe} = 51, N_{red} = 165).

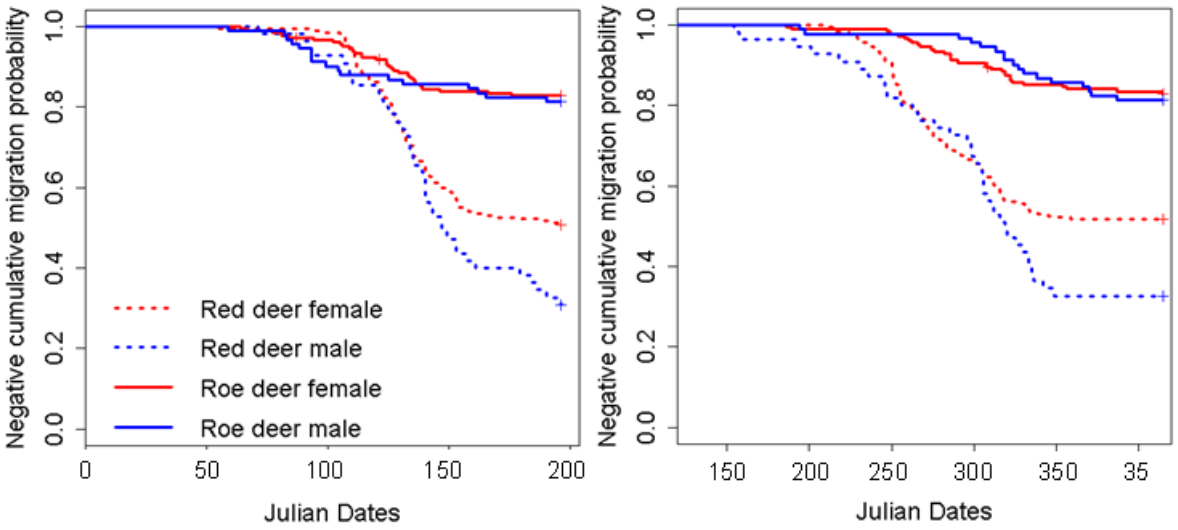


Figure 4-5. Estimated negative cumulative migration probability of roe deer (*Capreolus capreolus*, solid lines) and red (*Cervus elaphus*; dotted lines) deer migration for males (blue) and females (red) using time-to-event modeling for spring (left) and autumn (right). The graph represents the negative migration probability, i.e. a probability of 1 indicates 100% probability of residency, while 0 indicates 100% probability migration. We compared 154 female and 119 male roe deer and 170 female and 94 male red deer migration years. Populations spanned similar latitudinal gradient in Europe and GPS data were collected between 1999 and 2014.

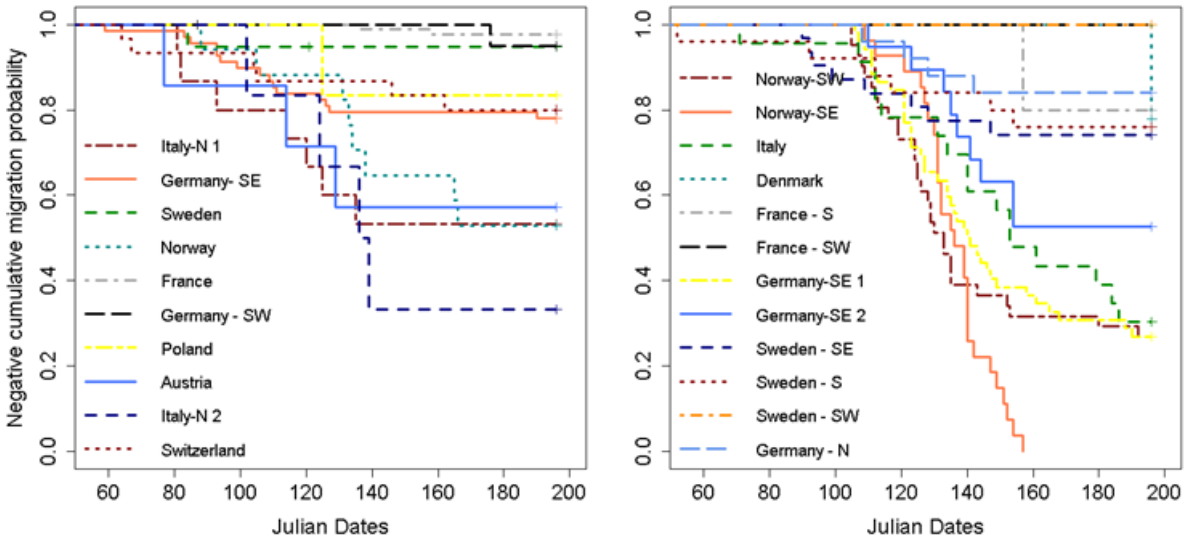


Figure 4-6. Estimated negative cumulative migration probability of roe (*Capreolus capreolus*; left) and red (*Cervus elaphus*; right) deer spring migration using time-to-event modeling for 10 roe deer and 12 red deer study areas. The graph represents the negative migration probability, i.e. a probability of 1 indicates 100% probability of residency, while 0 indicates 100% probability of migration. We compared 154 female and 119 male roe deer and 170 female and 94 male red deer migration years. Populations spanned a similar latitudinal gradient in Europe and GPS data were collected between 1999 and 2014.

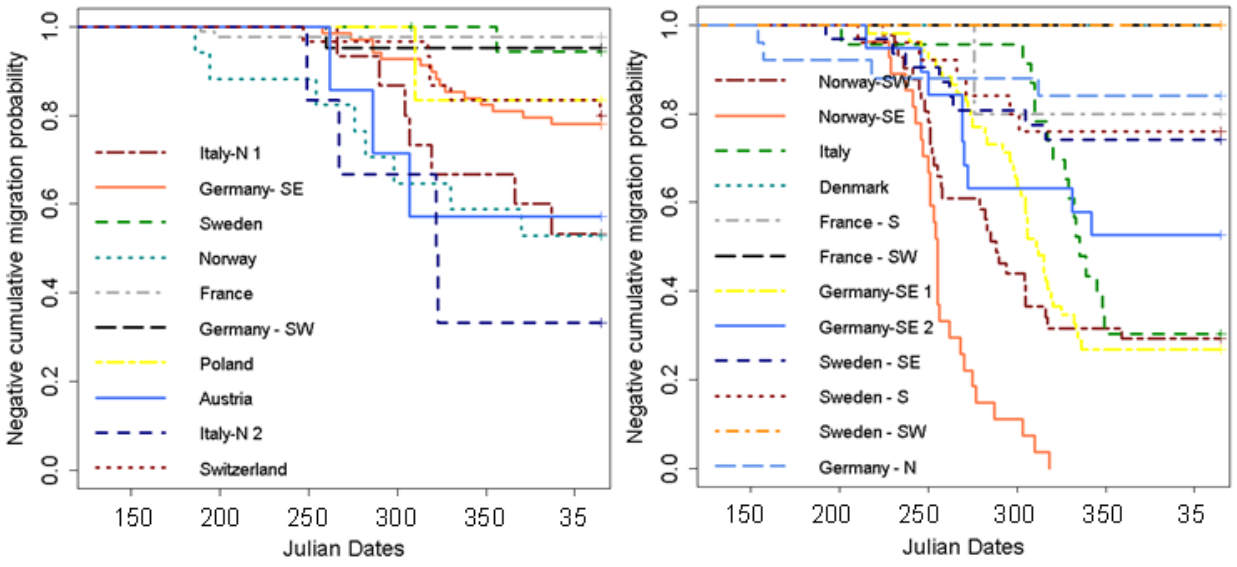


Figure 4-7. Estimated negative cumulative migration probability of roe (*Capreolus capreolus*; left) and red (*Cervus elaphus*; right) deer autumn migration using time-to-event modeling for 10 roe deer and 12 red deer study areas. The graph represents the negative migration probability, i.e. a probability of 1 indicates 100% probability of residency, while 0 indicates 100% probability of migration. We compared 154 female and 119 male roe deer and 170 female and 94 male red deer migration years. Populations spanned a similar latitudinal gradient in Europe and GPS data were collected between 1999 and 2014.

APPENDIX 4-A. Sample size and study area (SA) characteristics for roe deer (*Capreolus capreolus*; N = 273) global positioning data (GPS). Study area characteristics include the geographic location (latitude; Lat. and longitude; Long.), the years during which data used in this study were collected (Years), the number of total observation years (Obs.), the number of unique animals monitored (Animals), the number of migration events (Migrations). The following characteristics are given as averages by study area and their standard deviations in parentheses: elevation in m, slope in degrees, seasonality (contingency), between-year predictability (constancy), canopy closure (Canopy; %), proportion of forests landcover types (Forest; %), nightlights index, winter temperature (degrees C), winter snow depth (cm), Normalized Difference Vegetation Index (NDVI, range 0-1).

	Norway	**Sweden**	**Poland**	**Germany-SE**	**Germany - SW**	**Austria**	**Switzerland**	**Italy - N1**	**Italy - N2**	**France**
Lat.	60.69	58.15	52.68	48.95	48.47	47.45	46.59	46.02	46.08	43.29
Long.	8.85	12.43	23.48	13.35	8.17	15.07	7.55	11.04	10.76	0.89
Years	2008-2010	2007-2011	2008-2011	2006-2012	2010-2012	2009-2010	2012-2013	2005-2007	2013-2013	2003-2012
Obs.	18	19	6	68	21	7	31	15	6	86
Animals	15	17	6	51	20	7	22	15	6	83
Migrations	9	1	1	17	1	3	7	7	4	3
Elevation	393 (167.95)	89 (7.87)	163 (6.12)	762 (67.85)	280 (271.4)	1045 (99.75)	993 (208.27)	904 (284.43)	1047 (240.68)	315 (19.4)
Contingency	0.40 (0.03)	0.30 (0.02)	0.33 (0.03)	0.28 (0.04)	0.26 (0.03)	0.23 (0.01)	0.32 (0.03)	0.31 (0.05)	0.30 (0.03)	0.18 (0.02)

Appendix 4-A continued

Constancy	0.22	0.25	0.23	0.28	0.31	0.34	0.28	0.31	0.30	0.37
	(0.02)	(0.05)	(0.05)	(0.05)	(0.04)	(0.01)	(0.03)	(0.08)	(0.06)	(0.04)
Canopy	30.46	45.32	27.94	57.77	24.74	63.97	28.54	43.40	51.85	12.54
	(8.39)	(7.28)	(21.49)	(11.57)	(6.92)	(4.52)	(5.32)	(9.69)	(11.08)	(6.79)
Forest	30.55	53.26	42.33	78.01	26.57	95.14	29.97	67.53	75.83	10.58
	(19.53)	(20.5)	(41)	(25.4)	(14.86)	(6.52)	(18.48)	(20.98)	(19.34)	(17.38)
Slope	11.81	3.05	1.51	7.07	3.48	21.66	16.83	22.89	27.81	5.60
	(2.62)	(0.4)	(0.31)	(1.8)	(3.13)	(0.71)	(6.04)	(7.65)	(6.6)	(1.07)
Nightlights	43.27	3.04	8.67	4.13	8.03	1.18	10.49	24.08	11.60	0.87
	(13.15)	(0.52)	(3.54)	(4.11)	(3.87)	(1.66)	(7.22)	(16.38)	(13.23)	(0.46)
Temperature	-5.77	-0.29	-2.01	-0.51	3.91	-0.95	-1.59	1.82	0.93	7.15
	(2.02)	(2.34)	(1.8)	(1.68)	(1.27)	(0.65)	(1.78)	(1.87)	(0)	(0.86)
Snow depth	81.71	12.68	18.40	12.53	3.48	12.93	67.12	18.25	11.23	5.56
	(8.17)	(11.8)	(11.71)	(16.99)	(2.94)	(1.89)	(39.32)	(11.21)	(0)	(2.86)
NDVI	0.77	0.80	0.77	0.85	0.79	0.82	0.81	0.83	0.84	0.65
	0.04	0.03	0.05	0.02	0.03	0.01	0.02	0.02	0.03	0.07

APPENDIX 4-B. Sample size and study area (SA) characteristics for red deer (*Cervus elaphus,* N = 264) global positioning data (GPS). Study area characteristics include the geographic location (latitude; Lat. and longitude; Long.), the years during which data used in this study were collected (Years), the number of total observation years (Obs.)., number of unique animals monitored (Animals), the number of migration events (Migrations). The following characteristics are given as averages by study area and their standard deviations in parentheses: elevation in m, slope in degrees, seasonality (contingency), between-year predictability (constancy), canopy closure (Canopy; %), forests landcover types (Forest; %), nightlights index, winter temperature (degrees C), winter snow depth (cm), Normalized Difference Vegetation Index (NDVI, range 0-1).

SA	**Nor-way-SW**	**Nor-way-SE**	**Swe-den-SE**	**Swe-den-SW**	**Den-mark**	**Swe-den - S**	**Ger-many - N**	**Germ-any - SE 2**	**Germ-any - SE1**	**Italy**	**France - S**	**France - SW**
Lat.	61.35	60.61	58.78	58.33	55.93	55.64	53.96	49.04	48.94	46.44	44.33	42.85
Long.	6.09	8.66	16.50	12.48	9.31	13.84	10.00	13.34	13.46	10.51	3.76	0.53
Years	2005 - 2010	2009-2010	2006-2011	2008-2009	2006-2008	2007-2013	2008-2013	2005-2013	2002-2013	2005-2012	1999-200	2003
Obs.	41	27	31	5	9	25	25	19	52	23	5	2
Animals	40	15	14	3	8	13	16	18	43	13	5	2
Migrations	30	27	8	0	2	6	4	9	38	16	1	0
Elevation	261	662	60	120	86	82	36	826	872	1777	1184	1440
	-166.29	(157.9)	(11.79)	(6.51)	(15.4)	(51.26)	(15.72)	(87.34)	(85.59)	(205.1)	(162.3)	(15.39)
Slope	20.34	15.74	3.46	2.49	1.85	2.32	1.87	10.19	7.15	26.04	13.46	23.75
	(8.07)	(4.1)	(0.52)	(0.82)	(0.39)	(0.56)	(0.43)	(1.32)	(1.68)	(3.86)	(3.62)	(1.44)

Appendix 4-B continued

Contin-gency	0.35	0.39	0.30	0.28	0.24	0.29	0.23	0.26	0.30	0.33	0.28	0.34
	(0.03)	(0.03)	(0.02)	(0.01)	(0.03)	(0.03)	(0.02)	(0.03)	(0.03)	(0.06)	(0.06)	(0.04)
Constancy	0.22	0.25	0.29	0.33	0.32	0.25	0.32	0.28	0.24	0.25	0.37	0.20
	(0.04)	(0.06)	(0.03)	(0.02)	(0.05)	(0.05)	(0.04)	(0.04)	(0.02)	(0.05)	(0.06)	(0.04)
Canopy	37.43	45.23	54.54	62.40	43.89	39.67	44.25	66.83	58.20	33.06	51.86	30.07
	(11.91)	(10.24)	(2.82)	(2.46)	(13.7)	(12.38)	(18.19)	(4.9)	(6.93)	(11.94)	(7.04)	(9.6)
Forest %	62.6	77.0	81.0	97.4	53.4	56.3	54.3	92.1	87.2	53.4	91.8	38.5
	-21.7	-12.80	(8.57)	(4.34)	(30.8)	(25.01)	(36.54)	(10.01)	(17.27)	(19.25)	(7.79)	(14.85)
Nightlights	8.23	14.99	1.35	6.57	6.88	9.68	7.82	0.12	0.34	14.44	0.01	1.59
	(9.79)	(10.57)	(1.26)	(1.11)	(1.28)	(7.33)	(6.55)	(0.32)	(0.65)	(10.16)	(0.03)	(1.31)
Temp.	-1.46	-7.65	-1.10	1.47	2.06	2.14	1.45	-0.88	-0.18	-3.77	3.37	3.22
	(2.99)	(1.83)	(2.74)	(1.55)	(2.51)	(1.65)	(1.54)	(0.91)	(1.56)	(2.78)	(0.83)	(0.81)
Snow-depth	40.48	76.58	13.54	7.00	3.00	4.72	6.83	11.86	17.38	70.50	10.41	2.97
	(23.78)	(4.61)	(8.15)	(1.93)	(1.05)	(2.44)	(5.17)	(9.72)	(15.67)	(37.33)	(8.66)	(0.7)
NDVI	0.78	0.78	0.81	0.81	0.78	0.80	0.82	0.87	0.82	0.72	0.82	0.83
	(0.04)	(0.03)	(0.02)	(0.03)	(0.02)	(0.04)	(0.04)	(0.02)	(0.04)	(0.08)	(0.04)	(0.02)

APPENDIX 4-C. Information on individuals and Global Positioning System (GPS) collars for all roe deer (*Capreolus caprolus*) and red deer (*Cervus elaphus*), including species (spp.), country (C; IT = Italy, GR = Germany, SE = Sweden, NO = Norway, FR = France, AT = Austria, PL = Poland, DK = Denmark, CH = Switzerland), the study area (SA; if multiple populations were used from the same country the cardinal direction of the location of the population within the country is provided as identifier), animal ID (ID), the year from which data were used (Year), the sex (f = female, m = male), the first date of capture, the age class at capture (roe deer: 1 = fawn, 2 = yearling, 3 = adult; red deer: 1 = calf, 2 = yearling, 30 = adult, 31 = young adult between 24-60 months, males only; 32 = older adult, > 60 months, males only), the vendor of the fitted GPS collar, the average fix schedule during the monitoring year (Schedule), and the average GPS fix rate during the monitoring year (fix).

Spp.	C	SA	ID	Year	Sex	Capture Date	Age	Vendor	Schedule	Fix
roe	IT	Monte B. (N1)	767	2006	f	10/15/2005	3	Vectronic	5.00	0.62
roe	IT	Monte B. (N1)	770	2005	m	2/26/2005	3	Vectronic	2.25	0.78
roe	IT	Monte B. (N1)	771	2005	m	3/20/2005	3	Vectronic	2.25	0.90
roe	IT	Monte B. (N1)	772	2005	m	3/20/2005	3	Vectronic	4.00	0.78
roe	IT	Monte B. (N1)	774	2006	m	10/23/2005	3	Vectronic	4.00	0.87
roe	IT	Monte B. (N1)	782	2006	f	10/21/2005	3	Vectronic	4.00	0.92
roe	IT	Monte B. (N1)	783	2006	f	3/25/2006	3	Vectronic	4.00	0.68
roe	IT	Monte B. (N1)	784	2006	f	4/2/2006	2	Vectronic	4.00	0.71
roe	IT	Monte B. (N1)	785	2006	f	4/3/2006	3	Vectronic	4.00	0.22
roe	IT	Monte B. (N1)	789	2007	f	11/12/2006	3	Vectronic	4.00	0.87
roe	IT	Monte B. (N1)	791	2007	m	11/12/2006	3	Vectronic	4.00	0.92
roe	IT	Monte B. (N1)	792	2006	f	11/3/2005	3	Vectronic	4.00	0.91
roe	IT	Monte B. (N1)		2007			3	Vectronic	4.00	0.90
roe	IT	Monte B. (N1)	796	2005	f	2/26/2005	3	Vectronic	2.25	0.80
roe	IT	Monte B. (N1)	797	2005	f	2/27/2005	3	Vectronic	2.25	0.90
roe	IT	Monte B. (N1)	799	2005	f	3/20/2005	3	Vectronic	2.25	0.80
roe	IT	Monte B. (N1)	800	2005	f	4/2/2005	3	Vectronic	2.25	0.77

roe	IT	Monte B. (N1)	801	2005	f	4/2/2005	3	Vectronic	2.25	0.84
roe	GR	Bavarian NP (SE)	2	2007	m	3/26/2007	3	Vectronic	6.67	0.67
roe	GR	Bavarian NP (SE)	4	2006	m	3/14/2006	3	Vectronic	4.00	0.83
roe	GR	Bavarian NP (SE)	5	2007	m	12/2/2006	3	Vectronic	3.00	0.93
roe	GR	Bavarian NP (SE)	7	2007	m	11/10/2006	3	Vectronic	4.50	0.88
roe	GR	Bavarian NP (SE)	9	2005	f	3/10/2005	3	Vectronic	4.00	0.82
roe	GR	Bavarian NP (SE)	11	2006	f	2/1/2006	3	Vectronic	4.00	0.66
roe	GR	Bavarian NP (SE)	12	2006	m	2/3/2006	3	Vectronic	4.00	0.73
roe	GR	Bavarian NP (SE)		2008			3	Vectronic	7.00	0.96
roe	GR	Bavarian NP (SE)	14	2006	f	1/19/2006	3	Vectronic	4.00	0.76
roe	GR	Bavarian NP (SE)		2007			3	Vectronic	4.00	0.69
roe	GR	Bavarian NP (SE)		2009			3	/	1.00	1.00
roe	GR	Bavarian NP (SE)		2010			3	/	1.60	0.96
roe	GR	Bavarian NP (SE)	17	2008	f	12/4/2007	3	Vectronic	0.25	1.00
roe	GR	Bavarian NP (SE)		2009			3	/	4.50	0.99
roe	GR	Bavarian NP (SE)	18	2008	f	11/18/2007	3	Vectronic	7.00	0.83
roe	GR	Bavarian NP (SE)	19	2006	m	3/28/2006	3	Vectronic	4.00	0.82
roe	GR	Bavarian NP (SE)		2007			3	Vectronic	3.75	0.92
roe	GR	Bavarian NP (SE)	21	2008	m	12/31/2007	3	Vectronic	10.0	0.91
roe	GR	Bavarian NP (SE)	1367	2008	f	2/14/2008	2	Vectronic	1.00	0.95
roe	GR	Bavarian NP (SE)	1374	2008	f	2/8/2008	3	Vectronic	4.67	0.91
roe	GR	Bavarian NP (SE)		2009			3	Vectronic	0.50	0.96
roe	GR	Bavarian NP (SE)	1403	2008	m	11/28/2007	3	Vectronic	7.00	0.82
roe	GR	Bavarian NP (SE)	1415	2008	m	3/21/2008	3	Vectronic	7.00	0.97
roe	GR	Bavarian NP (SE)	1418	2009	m	2/3/2009	3	/	0.25	1.00
roe	GR	Bavarian NP (SE)	1431	2009	f	2/24/2009	3	Vectronic	0.50	0.94
roe	GR	Bavarian NP (SE)	1949	2012	f	2/17/2012	3	/	2.75	0.92
roe	GR	Bavarian NP (SE)	1950	2012	f	2/15/2012	3	/	2.75	0.91
roe	GR	Bavarian NP (SE)	1951	2012	m	2/1/2012	3	/	3.00	0.98
roe	GR	Bavarian NP (SE)	1952	2012	f	2/4/2011	3	Vectronic	3.00	0.95
roe	GR	Bavarian NP (SE)	1953	2012	f	2/22/2012	3	/	2.75	0.98
roe	GR	Bavarian NP (SE)	1954	2009	m	1/20/2009	3	Vectronic	4.83	0.88
roe	GR	Bavarian NP (SE)		2010			3	Vectronic	4.50	0.88
roe	GR	Bavarian NP (SE)	1956	2009	f	1/27/2009	3	Vectronic	4.83	0.99
roe	GR	Bavarian NP (SE)		2010			3	Vectronic	13.0	1.00
roe	GR	Bavarian NP (SE)	1958	2010	f	2/9/2010	3	/	3.00	0.99
roe	GR	Bavarian NP (SE)	1965	2009	f	1/8/2009	3	/	4.50	1.00
roe	GR	Bavarian NP (SE)		2010			3	/	6.50	1.00
roe	GR	Bavarian NP (SE)	1967	2007	m	3/7/2007	3	Vectronic	3.00	0.76
roe	GR	Bavarian NP (SE)	1970	2007	m	11/14/2006	3	/	2.00	0.72
roe	GR	Bavarian NP (SE)	1973	2010	f	3/17/2010	3	/	3.00	1.00
roe	GR	Bavarian NP (SE)	1975	2012	m	3/31/2011	3	/	3.00	0.93
roe	GR	Bavarian NP (SE)	1978	2009	m	12/9/2008	3	/	6.75	0.99

roe	GR	Bavarian NP (SE)		2010			3	/	6.33	0.99
roe	GR	Bavarian NP (SE)	1984	2007	m	1/27/2007	3	/	5.67	0.77
roe	GR	Bavarian NP (SE)	1985	2010	m	12/3/2009	3	/	2.33	0.98
roe	GR	Bavarian NP (SE)		2011			3	/	3.00	0.87
roe	GR	Bavarian NP (SE)	1987	2011	m	12/20/2010	3		3.00	0.98
roe	GR	Bavarian NP (SE)	1988	2008	f	10/31/2007	3	/	7.00	0.82
roe	GR	Bavarian NP (SE)	1995	2008	f	10/30/2007	3	Vectronic	7.00	0.88
roe	GR	Bavarian NP (SE)	1996	2008	f	2/19/2008	3	Vectronic	7.00	0.89
roe	GR	Bavarian NP (SE)		2010			3	Vectronic	3.00	0.99
roe	GR	Bavarian NP (SE)	1999	2009	f	1/27/2009	3	/	4.83	1.00
roe	GR	Bavarian NP (SE)		2010			3	/	6.50	0.99
roe	GR	Bavarian NP (SE)	2008	2009	m	11/28/2008	3	/	4.50	0.99
roe	GR	Bavarian NP (SE)	2010	2008	f	1/5/2008	3	/	7.00	0.99
roe	GR	Bavarian NP (SE)		2009			3	/	7.00	0.99
roe	GR	Bavarian NP (SE)	2011	2010	f	3/16/2010	3	/	3.00	0.99
roe	GR	Bavarian NP (SE)	2013	2010	f	3/16/2010	3	/	3.00	0.99
roe	GR	Bavarian NP (SE)	2015	2009	f	3/12/2009	2	/	4.83	1.00
roe	GR	Bavarian NP (SE)		2010			3	/	6.50	1.00
roe	GR	Bavarian NP (SE)	2016	2009	m	1/23/2009	3	/	4.83	0.99
roe	GR	Bavarian NP (SE)	2017	2010	f	3/5/2010	2	/	2.00	1.00
roe	GR	Bavarian NP (SE)	2018	2009	f	2/23/2009	3	/	4.83	0.98
roe	GR	Bavarian NP (SE)	2021	2009	f	3/4/2009	2	/	4.50	1.00
roe	GR	Bavarian NP (SE)		2010			3	/	6.50	1.00
roe	GR	Bavarian NP (SE)	2025	2012	m	1/16/2012	3	Vectronic	2.75	0.84
roe	GR	Bavarian NP (SE)	2026	2009	m	3/3/2009	3	/	4.83	0.99
roe	GR	Bavarian NP (SE)	2027	2009	m	3/6/2009	3	/	4.83	1.00
roe	GR	Bavarian NP (SE)	2030	2010	m	1/25/2010	3	/	3.00	0.98
roe	GR	Bavarian NP (SE)	2036	2011	m	2/03/2011	3	/	3.00	0.79
roe	GR	Bavarian NP (SE)	2037	2011	m	2/24/2011	3	/	3.00	0.98
roe	GR	Bavarian NP (SE)	2039	2009	m	4/15/2009	3	/	4.83	0.99
roe	SE	Koberg	828	2008	f	3/26/2008	2	Vectronic	2.50	1.00
roe	SE	Koberg	829	2007	m	1/24/2007	3	Vectronic	4.00	1.00
roe	SE	Koberg	831	2007	m	1/26/2007	2	Vectronic	4.00	0.99
roe	SE	Koberg	833	2007	f	1/25/2007	3	Vectronic	4.00	1.00
roe	SE	Koberg	836	2007	f	2/10/2007	3	Vectronic	4.00	0.97
roe	SE	Koberg	1358	2009	f	1/9/2009	3	Vectronic	4.00	0.99
roe	SE	Koberg	1359	2009	f	2/17/2009	3	Vectronic	2.25	0.98
roe	SE	Koberg	1361	2007	m	2/9/2007	3	Vectronic	4.00	0.96
roe	SE	Koberg	1363	2008	m	3/6/2008	3	Vectronic	4.00	0.95
roe	SE	Koberg		2009			3	Vectronic	2.25	0.99
roe	SE	Koberg	1364	2009	m	2/26/2009	3	Vectronic	2.25	0.99
roe	SE	Koberg	2315	2010	f	12/30/2009	3	Vectronic	2.25	1.00
roe	SE	Koberg	2318	2010	f	2/3/2010	3	Vectronic	2.25	1.00

roe	SE	Koberg	2324	2011	f	2/21/2011	3	Vectronic	2.25	1.00
roe	SE	Koberg	2325	2011	f	3/09/2011	3	Vectronic	2.25	0.99
roe	SE	Koberg	2327	2010	f	1/29/2010	3	Vectronic	2.25	0.99
roe	NO	Nina-west	837	2008	m	2/18/2008	3	ATS	4.50	1.00
roe	NO	Nina-west		2009			3	ATS	4.50	1.00
roe	NO	Nina-west	838	2008	f	3/6/2008	3	ATS	4.50	1.00
roe	NO	Nina-west	839	2008	f	3/10/2008	3	ATS	4.50	1.00
roe	NO	Nina-west	840	2008	f	3/17/2008	3	ATS	4.50	1.00
roe	NO	Nina-west	841	2008	f	3/28/2008	3	ATS	4.50	1.00
roe	NO	Nina-west	842	2008	f	4/4/2008	3	ATS	4.50	1.00
roe	NO	Nina-west	1333	2009	f	1/8/2009	3	Vectronic	3.00	1.00
roe	NO	Nina-west	1335	2009	f	1/20/2009	3	Vectronic	3.00	1.00
roe	NO	Nina-west		2010			3	Vectronic	9.00	1.00
roe	NO	Nina-west	1338	2009	m	2/10/2009	3	Vectronic	3.00	1.00
roe	NO	Nina-west		2010			3	Vectronic	9.00	1.00
roe	NO	Nina-west	1339	2009	m	2/11/2009	2	Vectronic	3.00	1.00
roe	NO	Nina-west		2010			3	Vectronic	9.00	1.00
roe	NO	Nina-west	1341	2009	m	4/3/2009	3	Vectronic	3.00	1.00
roe	NO	Nina-west	1343	2009	m	3/30/2009	3	Vectronic	2.00	1.00
roe	NO	Nina-west	1346	2009	m	4/1/2009	3	Vectronic	2.00	1.00
roe	NO	Nina-west	1347	2009	f	4/1/2009	3	Vectronic	2.00	1.00
roe	NO	Nina-west	1351	2010	f	3/6/2010	3	Tellus	9.00	1.00
roe	FR	Aurignac	1685	2005	f	1/13/2005	2	Lotek	3.00	0.87
roe	FR	Aurignac	1686	2005	f	1/20/2005	3	Lotek	3.00	0.92
roe	FR	Aurignac	1689	2005	m	1/6/2005	2	Lotek	3.00	0.91
roe	FR	Aurignac	1708	2005	f	2/3/2005	3	Lotek	3.00	0.96
roe	FR	Aurignac	1709	2005	m	2/3/2005	3	Lotek	3.00	0.93
roe	FR	Aurignac	1712	2005	f	2/3/2005	3	Lotek	3.00	0.93
roe	FR	Aurignac		2007			3	Lotek	2.33	0.97
roe	FR	Aurignac	1717	2005	f	2/9/2005	3	Lotek	3.00	0.95
roe	FR	Aurignac	1726	2006	m	1/12/2006	3	Lotek	2.33	0.89
roe	FR	Aurignac	1727	2006	m	1/12/2006	3	Lotek	2.33	0.90
roe	FR	Aurignac	1728	2006	f	1/12/2006	3	Lotek	2.33	0.87
roe	FR	Aurignac		2011			3	Lotek	2.33	0.92
roe	FR	Aurignac	1730	2006	f	1/12/2006	3	Lotek	2.33	0.95
roe	FR	Aurignac	1731	2006	f	1/12/2006	3	Lotek	2.33	0.81
roe	FR	Aurignac	1732	2006	f	1/5/2006	3	Lotek	2.33	0.85
roe	FR	Aurignac	1733	2006	f	1/19/2006	3	Lotek	2.33	0.96
roe	FR	Aurignac	1734	2006	f	1/19/2006	3	Lotek	2.33	0.96
roe	FR	Aurignac	1735	2006	m	1/19/2006	3	Lotek	2.33	0.95
roe	FR	Aurignac	1738	2006	m	1/26/2006	3	Lotek	2.33	0.92
roe	FR	Aurignac	1739	2006	m	1/26/2006	3	Lotek	2.33	0.97
roe	FR	Aurignac	1740	2006	m	2/2/2006	3	Lotek	2.33	0.89

roe	FR	Aurignac	1741	2006	m	1/5/2006	3	Lotek	2.33	0.95
roe	FR	Aurignac	1742	2006	m	2/2/2006	3	Lotek	2.33	0.88
roe	FR	Aurignac	1743	2006	f	2/2/2006	2	Lotek	2.33	0.93
roe	FR	Aurignac	1744	2007	f	1/11/2007	3	Lotek	2.33	0.96
roe	FR	Aurignac	1746	2007	f	1/11/2007	3	Lotek	2.33	0.94
roe	FR	Aurignac	1748	2007	f	1/11/2007	3	Lotek	2.33	0.92
roe	FR	Aurignac	1752	2007	f	2/1/2007	3	Lotek	2.33	0.93
roe	FR	Aurignac	1755	2007	f	2/1/2007	2	Lotek	2.33	0.95
roe	FR	Aurignac	1758	2007	f	2/8/2007	3	Lotek	2.33	0.97
roe	FR	Aurignac	1759	2007	m	2/8/2007	3	Lotek	2.33	0.94
roe	FR	Aurignac	1761	2007	f	2/8/2007	3	Lotek	2.33	0.96
roe	FR	Aurignac	1762	2007	f	2/8/2007	3	Lotek	2.33	0.92
roe	FR	Aurignac	1763	2007	f	2/8/2007	3	Lotek	2.33	0.89
roe	FR	Aurignac	1770	2008	f	1/10/2008	3	Lotek	2.33	0.88
roe	FR	Aurignac	1772	2008	f	1/17/2008	3	Lotek	2.33	0.93
roe	FR	Aurignac	1774	2008	f	1/10/2008	3	Lotek	2.33	0.94
roe	FR	Aurignac	1776	2008	m	1/10/2008	3	Lotek	2.33	0.95
roe	FR	Aurignac	1779	2008	f	1/24/2008	3	Lotek	2.33	0.93
roe	FR	Aurignac	1782	2008	f	1/31/2008	3	Lotek	2.33	0.88
roe	FR	Aurignac	1783	2003	f	3/14/2003	3	Lotek	4.00	0.57
roe	FR	Aurignac	1785	2008	f	1/31/2008	3	Lotek	2.33	0.87
roe	FR	Aurignac	1786	2008	f	1/31/2008	2	Lotek	2.33	0.91
roe	FR	Aurignac	1787	2010	m	2/4/2010	3	Lotek	0.50	0.96
roe	FR	Aurignac	1789	2008	f	2/7/2008	3	Lotek	2.33	0.94
roe	FR	Aurignac	1796	2003	f	2/18/2003	3	Lotek	3.00	0.90
roe	FR	Aurignac	1798	2003	f	2/18/2003	3	Lotek	3.00	0.92
roe	FR	Aurignac		2006			3	Lotek	2.33	0.98
roe	FR	Aurignac	1801	2009	f	1/22/2009	2	Lotek	2.33	0.90
roe	FR	Aurignac	1802	2009	m	1/29/2009	3	Lotek	2.33	0.91
roe	FR	Aurignac	1808	2009	m	1/29/2009	2	Lotek	2.33	0.89
roe	FR	Aurignac	1812	2009	m	1/29/2009	3	Lotek	0.50	0.80
roe	FR	Aurignac	1819	2012	f	3/1/2012	3	Lotek	0.50	0.97
roe	FR	Aurignac	1826	2009	m	2/26/2009	2	Lotek	0.50	0.94
roe	FR	Aurignac	1827	2011	f	2/03/2011	3		0.50	0.99
roe	FR	Aurignac	1829	2010	m	1/7/2010	3	Lotek	2.33	0.96
roe	FR	Aurignac	1831	2010	m	1/7/2010	3	Lotek	2.33	0.86
roe	FR	Aurignac	1834	2010	m	1/14/2010	3	Lotek	2.33	0.91
roe	FR	Aurignac	1835	2011	f	1/13/2010	3		2.33	0.86
roe	FR	Aurignac	1837	2010	f	1/14/2010	3	Lotek	2.33	0.91
roe	FR	Aurignac	1848	2010	f	1/21/2010	3	Lotek	0.50	0.98
roe	FR	Aurignac	1849	2010	m	1/28/2010	3	Lotek	0.50	0.84
roe	FR	Aurignac	1853	2010	f	1/28/2010	3	Lotek	0.50	0.96
roe	FR	Aurignac	1854	2010	m	2/4/2010	3	Lotek	0.50	0.99

roe	FR	Aurignac	1857	2011	f	/	3	/	2.33	0.96
roe	FR	Aurignac	1859	2011	m	/	3	/	2.33	0.83
roe	FR	Aurignac	1860	2011	m	/	3	/	2.33	0.81
roe	FR	Aurignac	1861	2011	m	/	3	/	2.33	0.89
roe	FR	Aurignac	1865	2011	m	/	3	/	2.33	0.95
roe	FR	Aurignac	1869	2011	m	/	3	/	2.33	0.88
roe	FR	Aurignac	1871	2011	f	/	3	/	2.33	0.71
roe	FR	Aurignac	1873	2011	f	/	3	/	2.33	0.90
roe	FR	Aurignac	1874	2011	f	/	3	/	0.50	0.93
roe	FR	Aurignac	1875	2011	f	/	3	/	0.50	0.97
roe	FR	Aurignac	1881	2011	f	/	3	/	0.50	0.97
roe	FR	Aurignac	1882	2011	f	/	2	/	0.50	0.97
roe	FR	Aurignac	1890	2012	m	1/5/2012	3	Lotek	0.50	0.95
roe	FR	Aurignac	1897	2012	m	1/12/2012	3	Lotek	0.50	0.96
roe	FR	Aurignac	1900	2012	f	1/12/2012	2	Lotek	0.50	0.96
roe	FR	Aurignac	1901	2012	m	1/17/2012	3	Lotek	2.33	0.88
roe	FR	Aurignac	1903	2012	f	1/17/2012	3	Lotek	2.33	0.93
roe	FR	Aurignac	1906	2012	f	1/26/2012	3	Lotek	0.50	0.98
roe	FR	Aurignac	1912	2012	f	1/26/2012	3	Lotek	0.50	0.98
roe	FR	Aurignac	1914	2012	m	1/26/2012	3	Lotek	0.50	0.93
roe	FR	Aurignac	1917	2012	f	2/2/2012	3	Lotek	0.50	0.75
roe	FR	Aurignac	1920	2003	m	1/30/2003	3	Lotek	3.00	0.87
roe	FR	Aurignac	1921	2003	f	2/5/2003	3	Lotek	3.00	0.75
roe	FR	Aurignac	1922	2003	m	2/12/2003	3	Lotek	3.00	0.83
roe	FR	Aurignac	1924	2003	m	2/18/2003	3	Lotek	3.00	0.88
roe	FR	Aurignac	1925	2003	f	2/18/2003	3	Lotek	3.00	0.96
roe	FR	Aurignac	1926	2003	m	2/18/2003	3	Lotek	3.00	0.87
roe	FR	Aurignac	1929	2003	f	3/11/2003	3	Lotek	4.00	0.63
roe	GR	Baden-W. (SW)	1453	2010	f	2/22/2010	3	E-OBS	0.25	0.97
roe	GR	Baden-W. (SW)	2041	2011	f	/	3	/	0.25	0.99
roe	GR	Baden-W. (SW)	2043	2011	f	/	3	/	0.25	1.00
roe	GR	Baden-W. (SW)	2044	2011	f	/	3	/	0.25	0.99
roe	GR	Baden-W. (SW)	2045	2011	f	/	3	/	0.25	0.99
roe	GR	Baden-W. (SW)	2047	2011	m	/	2	/	0.25	0.99
roe	GR	Baden-W. (SW)	2048	2012	m	1/5/2011	2	E-OBS	0.25	0.99
roe	GR	Baden-W. (SW)	2049	2011	f	/	2	/	0.25	0.99
roe	GR	Baden-W. (SW)	2054	2012	f	11/17/2011	3	E-OBS	0.25	1.00
roe	GR	Baden-W. (SW)	2055	2012	f	12/1/2011	3	E-OBS	0.25	0.99
roe	GR	Baden-W. (SW)	2056	2012	f	12/2/2011	3	E-OBS	0.25	0.99
roe	GR	Baden-W. (SW)	2061	2012	m	12/20/2011	2	E-OBS	0.83	0.98
roe	GR	Baden-W. (SW)	2066	2012	f	2/2/2012	3	E-OBS	0.25	1.00
roe	GR	Baden-W. (SW)	2067	2012	f	2/2/2012	2	E-OBS	0.25	1.00
roe	GR	Baden-W. (SW)	2069	2012	f	2/7/2012	3	E-OBS	0.25	1.00

roe	GR	Baden-W. (SW)	2070	2012	f	2/9/2012	2	E-OBS	0.25	0.99
roe	GR	Baden-W. (SW)	2072	2012	f	2/10/2012	2	E-OBS	0.25	0.99
roe	GR	Baden-W. (SW)	2074	2012	f	2/13/2012	2	E-OBS	0.25	0.99
roe	GR	Baden-W. (SW)	2075	2012	f	2/22/2012	3	E-OBS	0.25	1.00
roe	GR	Baden-W. (SW)	2078	2012	f	3/14/2012	2	E-OBS	0.25	1.00
roe	GR	Baden-W. (SW)	2079	2012	f	3/28/2012	2	E-OBS	0.25	1.00
roe	PL	Bialowieza	1476	2008	f	3/31/2008	3	Vectronic	2.50	0.98
roe	PL	Bialowieza	1478	2010	f	1/18/2010	3	Vectronic	2.50	1.00
roe	PL	Bialowieza	1482	2010	f	1/27/2010	3	Vectronic	2.50	1.00
roe	PL	Bialowieza	1485	2011	f	/	3	/	2.50	1.00
roe	PL	Bialowieza	1487	2011	f	/	3	/	2.50	0.99
roe	PL	Bialowieza	1489	2011	f	/	3	/	2.50	0.99
roe	AT	Loeben	1494	2009	f	12/20/2008	3	Vectronic	3.25	0.98
roe	AT	Loeben	1498	2009	m	11/3/2008	2	Vectronic	3.25	0.91
roe	AT	Loeben	1504	2010	f	12/4/2009	3	Vectronic	2.17	0.99
roe	AT	Loeben	1505	2010	m	12/4/2009	3	Vectronic	2.17	0.98
roe	AT	Loeben	1507	2009	f	11/12/2008	3	Vectronic	3.25	0.99
roe	AT	Loeben	1509	2009	f	11/9/2007	3	Vectronic	3.25	1.00
roe	AT	Loeben	1514	2009	m	11/13/2008	2	Vectronic	3.25	0.98
roe	IT	Val R. (N2)	1606	2013	f	12/17/2012	3	Vectronic	3.00	0.99
roe	IT	Val R. (N2)	1607	2013	f	12/18/2012	2	Vectronic	3.00	0.99
roe	IT	Val R. (N2)	1610	2013	f	12/20/2012	3	Vectronic	3.00	0.99
roe	IT	Val R. (N2)	1611	2013	f	1/7/2013	3	Vectronic	3.00	0.99
roe	IT	Val R. (N2)	1618	2013	f	2/13/2013	3	Vectronic	3.00	0.99
roe	IT	Val R. (N2)	1621	2013	f	2/15/2013	3	Vectronic	3.00	0.98
roe	IT	Val R. (N2)	1623	2013	m	2/28/2013	2	Vectronic	3.00	0.97
roe	CH	Bernese	2239	2012	f	11/29/2011	3	E-OBS	0.50	0.99
roe	CH	Bernese		2013			3	E-OBS	0.50	0.99
roe	CH	Bernese	2240	2012	m	2/25/2012	2	E-OBS	0.50	0.99
roe	CH	Bernese		2013			2	E-OBS	0.50	0.99
roe	CH	Bernese	2241	2012	f	3/1/2012	3	E-OBS	0.50	0.99
roe	CH	Bernese		2013			3	E-OBS	0.50	0.99
roe	CH	Bernese	2242	2012	m	3/9/2012	3	E-OBS	0.50	0.99
roe	CH	Bernese		2013			3	E-OBS	0.50	0.99
roe	CH	Bernese	2244	2012	f	3/24/2012	3	E-OBS	0.50	0.98
roe	CH	Bernese		2013			3	E-OBS	0.50	0.98
roe	CH	Bernese	2247	2012	f	11/29/2011	2	E-OBS	0.50	1.00
roe	CH	Bernese		2013			2	E-OBS	0.50	0.99
roe	CH	Bernese	2248	2012	f	3/22/2012	3	E-OBS	0.50	0.98
roe	CH	Bernese	2249	2012	f	12/15/2011	3	E-OBS	0.50	0.99
roe	CH	Bernese		2013			3	E-OBS	0.50	0.99
roe	CH	Bernese	2252	2013	f	1/24/2013	3	E-OBS	0.50	0.98
roe	CH	Bernese	2253	2013	f	2/9/2013	3	E-OBS	0.50	0.99

roe	CH	Bernese	2256	2013	f	3/14/2013	3	E-OBS	0.50	0.99
roe	CH	Bernese	2260	2013	m	11/20/2012	3	E-OBS	0.50	0.99
roe	CH	Bernese	2264	2013	f	11/30/2012	3	E-OBS	0.50	0.99
roe	CH	Bernese	2274	2013	f	1/18/2013	3	E-OBS	0.50	0.99
roe	CH	Bernese	2279	2013	m	1/25/2013	2	E-OBS	0.50	0.99
roe	CH	Bernese	2282	2013	f	2/2/2013	3	E-OBS	0.50	0.99
roe	CH	Bernese	2283	2013	f	2/5/2013	2	E-OBS	0.50	0.99
roe	CH	Bernese	2285	2013	m	2/7/2013	3	E-OBS	0.50	0.98
roe	CH	Bernese	2288	2013	f	2/7/2013	3	E-OBS	0.50	0.99
roe	CH	Bernese	2294	2013	f	2/21/2013	3	E-OBS	0.50	0.99
roe	CH	Bernese	2295	2013	f	2/28/2013	3	E-OBS	0.50	0.99
roe	CH	Bernese	2296	2012	f	3/23/2012	3	E-OBS	0.50	0.99
roe	CH	Bernese		2013			3	E-OBS	0.50	0.99
roe	CH	Bernese	2298	2012	f	2/25/2012	3	E-OBS	0.50	0.99
roe	CH	Bernese		2013			3	E-OBS	0.50	0.99
roe	CH	Bernese	2301	2013	f	3/16/2013	3	E-OBS	0.50	0.99
roe	CH	Bernese	2305	2013	m	4/4/2013	2	E-OBS	0.50	0.99
red	NO	Sunnf. (SW)	26	2009	f	2/5/2009	30	Televilt	1.00	1.00
red	NO	Sunnf. (SW)		2010			30	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	27	2009	f	2/18/2009	30	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	30	2005	f	1/29/2005	/	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	31	2005	f	1/29/2005	/	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	33	2010	m	3/24/2009	31	Televilt	1.50	1.00
red	NO	Sunnf. (SW)	41	2010	f	2/4/2010	30	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	44	2010	f	2/15/2010	30	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	46	2005	f	1/29/2005	/	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	49	2010	f	3/6/2010	30	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	51	2010	f	3/8/2010	30	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	53	2010	f	3/23/2010	30	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	54	2010	f	3/30/2010	30	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	56	2005	f	1/29/2005	2	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	57	2005	f	2/18/2005	/	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	58	2005	f	2/18/2005	/	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	59	2005	f	2/18/2005	/	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	60	2005	f	3/4/2005	/	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	61	2008	f	4/17/2008	30	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	64	2005	f	3/4/2005	/	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	65	2005	f	3/4/2005	/	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	66	2005	f	3/4/2005	/	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	67	2005	f	3/6/2005	/	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	68	2005	f	3/9/2005	/	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	69	2005	f	1/23/2005	/	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	70	2006	f	2/28/2006	30	Televilt	1.00	1.00

red	NO	Sunnf. (SW)	71	2006	f	2/28/2006	30	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	73	2006	f	3/1/2006	30	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	76	2006	f	3/8/2006	2	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	78	2005	f	1/23/2005	/	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	80	2006	f	3/20/2006	2	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	81	2006	f	3/20/2006	30	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	83	2006	f	3/8/2006	30	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	84	2005	f	1/23/2005	/	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	87	2007	f	3/4/2007	/	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	89	2007	f	3/4/2007	/	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	94	2005	f	1/26/2005	/	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	96	2008	m	6/27/2007	30	Televilt	1.50	1.00
red	NO	Sunnf. (SW)	99	2005	f	1/26/2005	/	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	103	2007	f	4/11/2007	2	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	107	2005	f	1/26/2005	/	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	108	2007	f	5/9/2007	/	Televilt	1.00	1.00
red	NO	Sunnf. (SW)	109	2007	f	5/9/2007	/	Televilt	1.00	1.00
red	NO	Buskerud (SE)	2	2009	f	3/16/2009	/	Vectronic	1.00	1.00
red	NO	Buskerud (SE)		2010				Vectronic	1.00	1.00
red	NO	Buskerud (SE)	3	2009	f	2/22/2009	/	Vectronic	1.00	1.00
red	NO	Buskerud (SE)		2010				Vectronic	1.00	1.00
red	NO	Buskerud (SE)	5	2009	f	2/23/2009	/	Vectronic	1.00	1.00
red	NO	Buskerud (SE)		2010				Vectronic	1.00	1.00
red	NO	Buskerud (SE)	6	2009	f	3/4/2009	/	Vectronic	1.00	1.00
red	NO	Buskerud (SE)		2010				Vectronic	1.00	1.00
red	NO	Buskerud (SE)	7	2009	f	3/4/2009	/	Vectronic	1.00	0.99
red	NO	Buskerud (SE)		2010				Vectronic	1.00	0.99
red	NO	Buskerud (SE)	8	2009	f	3/11/2009	/	Vectronic	1.00	0.99
red	NO	Buskerud (SE)		2010				Vectronic	1.00	0.99
red	NO	Buskerud (SE)	9	2009	f	3/15/2009	/	Vectronic	1.00	0.98
red	NO	Buskerud (SE)		2010				Vectronic	1.00	1.00
red	NO	Buskerud (SE)	11	2009	f	2/24/2009	/	Vectronic	1.00	1.00
red	NO	Buskerud (SE)		2010				Vectronic	1.00	1.00
red	NO	Buskerud (SE)	12	2009	f	2/24/2009	/	Vectronic	1.00	1.00
red	NO	Buskerud (SE)		2010				Vectronic	1.00	0.99
red	NO	Buskerud (SE)	13	2009	f	3/3/2009	/	Vectronic	1.00	1.00
red	NO	Buskerud (SE)		2010				Vectronic	1.00	1.00
red	NO	Buskerud (SE)	15	2010	f	3/4/2009	/	Vectronic	1.00	0.99
red	NO	Buskerud (SE)	17	2009	f	3/15/2009	/	Vectronic	1.00	0.93
red	NO	Buskerud (SE)	18	2009	f	3/16/2009	/	Vectronic	1.00	1.00
red	NO	Buskerud (SE)		2010				Vectronic	1.00	1.00
red	NO	Buskerud (SE)	20	2009	f	3/17/2009	/	Vectronic	1.00	1.00
red	NO	Buskerud (SE)		2010	f	3/17/2009	/	Vectronic	1.00	0.98

red	NO	Buskerud (SE)	21	2010	m	3/11/2010	/	Vectronic	1.50	0.97
red	IT	Stelvio NP	111	2011	f		30		1.00	0.86
red	IT	Stelvio NP	113	2008	m	10/1/2007	31	Vectronic	4.00	0.99
red	IT	Stelvio NP		2009			31	Vectronic	4.00	1.00
red	IT	Stelvio NP		2010			31	Vectronic	2.50	0.99
red	IT	Stelvio NP	116	2009	m	10/8/2008	32	Vectronic	4.00	0.98
red	IT	Stelvio NP		2010			32	Vectronic	2.50	0.99
red	IT	Stelvio NP	117	2010	f	10/7/2009	30	Vectronic	2.50	1.00
red	IT	Stelvio NP		2011			30		2.50	0.96
red	IT	Stelvio NP	119	2006	f	10/6/2005	30	Televilt	0.75	1.00
red	IT	Stelvio NP	120	2005	f	4/28/2005	30	Televilt	0.75	0.92
red	IT	Stelvio NP		2006	f		30		0.75	0.93
red	IT	Stelvio NP	121	2012	f	1/18/2012	30	Vectronic	4.00	0.87
red	IT	Stelvio NP	122	2010	f	10/20/2009	2	Vectronic	4.00	0.96
red	IT	Stelvio NP		2011			30		2.50	0.94
red	IT	Stelvio NP	127	2008	m	10/5/2007	32	Vectronic	2.50	0.99
red	IT	Stelvio NP	128	2006	m	10/4/2005	32	Televilt	0.75	1.00
red	IT	Stelvio NP	135	2011			32		1.00	0.82
red	IT	Stelvio NP	137	2010	f	10/8/2009	30	Vectronic	2.50	0.94
red	IT	Stelvio NP		2011			30		2.50	0.94
red	IT	Stelvio NP	138	2010	f	10/9/2009	30	Vectronic	2.50	0.91
red	DK	Store H.	161	2007	f	3/6/2007	2	Lotek	0.50	0.97
red	DK	Store H.	162	2006	f	3/15/2006	30	Lotek	0.50	0.92
red	DK	Store H.	163	2006	f	3/15/2006	30	Lotek	1.00	0.94
red	DK	Store H.	164	2006	f	3/15/2006	30	Lotek	1.00	0.94
red	DK	Store H.		2007	f		30		1.00	0.94
red	DK	Store H.	165	2006	f	4/12/2006	30	Lotek	1.00	0.95
red	DK	Store H.	166	2007	m	3/6/2007	2	Lotek	0.50	0.95
red	DK	Store H.	167	2007	f	3/6/2007	2	Lotek	0.50	0.97
red	DK	Store H.	168	2008	f	3/21/2008	2	Lotek	1.00	0.95
red	DK	Store H.	169	2008	m	3/2/2008	2	Lotek	1.00	0.91
red	FR	Cavennes (S)	154	2000	f	10/13/1999	30	Lotek	1.50	0.89
red	FR	Cavennes (S)	155	1999	m	11/22/1998	30	Lotek	1.50	0.92
red	FR	Cavennes (S)	157	2000	m	12/10/1999	30	Lotek	1.50	0.93
red	FR	Cavennes (S)	158	2000	f	3/27/2000	30	Lotek	1.50	0.63
red	FR	Cavennes (S)	160	1999	f	11/6/1998	1	Lotek	1.50	0.81
red	FR	Pyrenees (SW)	144	2003	f	4/18/2003	30	Lotek	1.50	0.89
red	FR	Pyrenees (SW)	148	2003	m	4/15/2003	30	Lotek	1.50	0.72
red	GR	Rachel(SE 2)	287	2012	m	2/23/2012	31	Vectronic	0.75	0.99
red	GR	Rachel(SE 2)	288	2008	f	2/28/2008	1	Vectronic	1.25	0.99
red	GR	Rachel(SE 2)		2009			2		0.25	1.00
red	GR	Rachel(SE 2)	290	2008	m	4/4/2008	31	Vectronic	0.83	1.00
red	GR	Rachel(SE 2)	291	2011	f	2/3/2011	2		0.75	1.00

red	GR	Rachel(SE 2)	292	2008	f	4/4/2008	30	Vectronic	0.83	0.99
red	GR	Rachel(SE 2)	297	2008	f	8/27/2007	2	Vectronic	2.50	0.96
red	GR	Rachel(SE 2)	299	2007	f	4/12/2007	1	Vectronic	1.75	0.99
red	GR	Rachel(SE 2)	301	2005	f	4/17/2005	30	Vectronic	3.00	0.71
red	GR	Rachel(SE 2)	303	2003	f	4/30/2003	30	Vectronic	3.00	0.93
red	GR	Rachel(SE 2)	306	2011	f	9/9/2010	30	/	0.50	0.98
red	GR	Rachel(SE 2)	310	2011	f	4/15/2010	30	/	0.25	0.97
red	GR	Rachel(SE 2)	312	2007	f	4/12/2007	1	Vectronic	1.75	0.99
red	GR	Rachel(SE 2)		2008			2	Vectronic	2.50	0.99
red	GR	Rachel(SE 2)	313	2013	f	3/27/2013	30	Vectronic	1.00	1.00
red	GR	Rachel(SE 2)	314	2002	f	4/24/2002	30	Vectronic	3.00	0.91
red	GR	Rachel(SE 2)		2003			30	Vectronic	2.50	0.72
red	GR	Rachel(SE 2)		2005			30	Vectronic	2.00	0.76
red	GR	Rachel(SE 2)	344	2013	f	2/28/2011	30	Vectronic	1.00	1.00
red	GR	Rachel(SE 2)	349	2005	m	4/17/2005	32	Vectronic	1.00	0.88
red	GR	Rachel(SE 2)	353	2006	F	3/2/2006	30	Vectronic	1.00	0.90
red	GR	Rachel(SE 2)	354	2004	f	5/3/2004	30	Vectronic	2.00	0.78
red	GR	Rachel(SE 2)	355	2002	m	3/27/2002	32	Vectronic	3.00	0.89
red	GR	Rachel(SE 2)	358	2008	m	4/4/2008	32	Vectronic	1.25	0.58
red	GR	Rachel(SE 2)	360	2008	f	4/28/2008	1	Vectronic	1.25	0.99
red	GR	Rachel(SE 2)	361	2008	m	2/28/2008	2	Vectronic	1.25	0.96
red	GR	Rachel(SE 2)	366	2008	f	2/28/2008	30	Vectronic	1.50	0.85
red	GR	Rachel(SE 2)	367	2008	f	4/28/2008	30	Vectronic	1.25	1.00
red	GR	Rachel(SE 2)		2009			30	Vectronic	0.25	1.00
red	GR	Rachel(SE 2)	371	2011	f	4/15/2011	30	/	0.75	1.00
red	GR	Rachel(SE 2)	375	2005	m	3/14/2002	32	Vectronic	2.00	0.56
red	GR	Rachel(SE 2)		2006			32	Vectronic	2.00	0.58
red	GR	Rachel(SE 2)	376	2011	f	4/15/2011	30		0.75	0.99
red	GR	Rachel(SE 2)		2012			30	Vectronic	0.75	0.99
red	GR	Rachel(SE 2)	377	2004	m	4/7/2004	32	Vectronic	2.00	0.95
red	GR	Rachel(SE 2)	380	2006	f	4/7/2006	2	Vectronic	1.00	0.94
red	GR	Rachel(SE 2)		2007			30	Vectronic	13.0	0.83
red	GR	Rachel(SE 2)	381	2004	m	3/19/2003	32	Vectronic	1.33	0.28
red	GR	Rachel(SE 2)	382	2007	f	4/12/2007	1	Vectronic	1.75	0.99
red	GR	Rachel(SE 2)	383	2008	m	4/14/2008	32	Vectronic	1.50	0.99
red	GR	Rachel(SE 2)	393	2013	f	2/28/2013	30	Vectronic	1.00	1.00
red	GR	Rachel(SE 2)	395	2013	f	2/28/2013	30	Vectronic	1.00	1.00
red	GR	Rachel(SE 2)	396	2013	f	3/27/2013	30	Vectronic	1.00	0.89
red	GR	Rachel(SE 2)	397	2013	f	3/27/2013	30	Vectronic	1.00	1.00
red	GR	Rachel(SE 2)	398	2013	f	3/27/2013	30	Vectronic	1.00	0.75
red	GR	Falken.(SE 1)	293	2008	f	2/20/2008	1	Vectronic	1.25	0.94
red	GR	Falken.(SE 1)		2009			2	Vectronic	0.83	0.99
red	GR	Falken.(SE 1)	294	2010	m	3/17/2010	31	Vectronic	0.50	1.00

red	GR	Falken.(SE 1)	304	2005	m	5/5/2005	31	Vectronic	1.00	0.78
red	GR	Falken.(SE 1)	309	2013	f	1/24/2013	30	Vectronic	1.00	0.92
red	GR	Falken.(SE 1)	346	2009	f	3/24/2009	30	Vectronic	1.00	0.92
red	GR	Falken.(SE 1)	347	2010	m	2/23/2010	31	Vectronic	0.50	1.00
red	GR	Falken.(SE 1)	369	2007	m	1/10/2007	2	Vectronic	2.50	0.75
red	GR	Falken.(SE 1)		2008			31	Vectronic	3.50	0.79
red	GR	Falken.(SE 1)	370	2009	f	3/20/2009	1	Vectronic	1.25	0.94
red	GR	Falken.(SE 1)	378	2005	m	5/10/2005	31	Vectronic	1.00	0.93
red	GR	Falken.(SE 1)	385	2008	m	4/11/2008	2	Vectronic	1.25	0.99
red	GR	Falken.(SE 1)	387	2013	f	1/24/2013	30	Vectronic	1.00	0.99
red	GR	Falken.(SE 1)	388	2013	f	3/20/2013	30	Vectronic	1.00	0.64
red	GR	Falken.(SE 1)	389	2013	f	2/18/2013	30	Vectronic	1.00	0.87
red	GR	Falken.(SE 1)	390	2013	f	12/19/2012	30	Vectronic	1.00	0.98
red	GR	Falken.(SE 1)	391	2013	f	1/31/2013	30	Vectronic	1.00	0.99
red	GR	Falken.(SE 1)	392	2013	f	3/4/2013	30	Vectronic	1.00	1.00
red	GR	Falken.(SE 1)	394	2013	f	2/28/2013	30	Vectronic	1.00	1.00
red	GR	Falken.(SE 1)	399	2013	f	3/15/2013	30	Vectronic	1.00	0.99
red	SE	Komaren (SE)	401	2009	f	4/2/2009	30	Vectronic	1.50	0.91
red	SE	Komaren (SE)		2010			30	Vectronic	4.00	0.91
red	SE	Komaren (SE)	402	2010	m	2/4/2010	32	Vectronic	4.00	0.93
red	SE	Komaren (SE)	403	2010	m	2/16/2010	32	Vectronic	4.00	0.94
red	SE	Komaren (SE)		2011			32		4.00	0.94
red	SE	Komaren (SE)	405	2010	f	2/25/2010	30	Vectronic	4.00	0.99
red	SE	Komaren (SE)		2011			30		4.00	0.98
red	SE	Komaren (SE)	406	2010	f	2/25/2010	30	Vectronic	4.00	1.00
red	SE	Komaren (SE)		2011			30		4.00	1.00
red	SE	Komaren (SE)	407	2011	m	2/15/2011	32	/	4.00	0.99
red	SE	Komaren (SE)	419	2006	f	2/7/2006	30	Vectronic	1.83	0.84
red	SE	Komaren (SE)	420	2006	f	2/8/2006	30	Vectronic	4.50	0.94
red	SE	Komaren (SE)		2007			30		1.00	0.99
red	SE	Komaren (SE)		2008			30		0.25	0.98
red	SE	Komaren (SE)	430	2006	f	2/15/2006	30	Vectronic	5.00	0.76
red	SE	Komaren (SE)		2007			30	Vectronic	1.00	0.94
red	SE	Komaren (SE)		2008			30	Vectronic	0.25	0.97
red	SE	Komaren (SE)	431	2006	f	2/20/2006	30	Vectronic	1.83	0.99
red	SE	Komaren (SE)		2007			30	Vectronic	1.00	0.98
red	SE	Komaren (SE)		2008			30	Vectronic	0.25	1.00
red	SE	Komaren (SE)	432	2006	f	2/28/2006	30	Vectronic	5.00	0.90
red	SE	Komaren (SE)		2007			30	Vectronic	1.00	0.98
red	SE	Komaren (SE)		2008			30	Vectronic	1.50	0.98
red	SE	Komaren (SE)	433	2006	f	3/5/2006	30	Vectronic	1.83	0.94
red	SE	Komaren (SE)		2007			30	Vectronic	1.00	0.97
red	SE	Komaren (SE)		2008			30	Vectronic	0.25	0.99

red	SE	Komaren (SE)	434	2006	f	3/7/2006	30	Vectronic	1.83	0.90
red	SE	Komaren (SE)		2007			30	Vectronic	1.00	0.96
red	SE	Komaren (SE)		2008			30	Vectronic	0.25	0.99
red	SE	Komaren (SE)	435	2006	f	3/7/2006	30	Vectronic	1.83	0.98
red	SE	Komaren (SE)		2007			30	Vectronic	1.00	0.99
red	SE	Komaren (SE)		2008			30	Vectronic	0.25	0.99
red	SE	Komaren (SE)		2009			30	Vectronic	4.17	0.99
red	SE	Komaren (SE)	436	2006	f	3/8/2006	30	Vectronic	1.83	0.98
red	SE	Komaren (SE)	437	2007	m	2/10/2007	32	Vectronic	1.83	1.00
red	SE	Komaren (SE)		2008			32	Vectronic	1.50	1.00
red	SE	Komaren (SE)	438	2007	m	2/15/2007	32	Vectronic	1.83	1.00
red	SE	Komaren (SE)		2008			32	Vectronic	1.50	1.00
red	SE	Komaren (SE)	440	2007	m	3/11/2007	32	Vectronic	1.83	1.00
red	SE	Komaren (SE)	441	2008	m	9/13/2007	32	Vectronic	1.50	0.98
red	SE	Komaren (SE)		2009			32	Vectronic	1.50	0.98
red	SE	Skane (S)	408	2007	f	2/11/2007	30	Vectronic	4.00	0.97
red	SE	Skane (S)	409	2007	f	2/12/2007	30	Vectronic	1.83	0.99
red	SE	Skane (S)		2008			30	Vectronic	1.50	0.99
red	SE	Skane (S)	410	2007	f	2/25/2007	30	Vectronic	4.00	1.00
red	SE	Skane (S)		2008			30	Vectronic	1.50	0.99
red	SE	Skane (S)		2009			30	Vectronic	4.17	1.00
red	SE	Skane (S)	411	2007	f	2/27/2007	30	Vectronic	2.83	0.98
red	SE	Skane (S)	412	2007	f	3/7/2007	30	Vectronic	2.83	0.99
red	SE	Skane (S)		2008			30	Vectronic	1.50	1.00
red	SE	Skane (S)	413	2007	f	3/8/2007	30	Vectronic	2.83	1.00
red	SE	Skane (S)		2008			30	Vectronic	1.50	1.00
red	SE	Skane (S)		2009			30	Vectronic	4.17	0.99
red	SE	Skane (S)	414	2008	f	2/26/2008	30	Vectronic	1.50	0.99
red	SE	Skane (S)	415	2008	f	3/1/2008	30	Vectronic	1.50	0.99
red	SE	Skane (S)		2009			30	Vectronic	1.50	0.99
red	SE	Skane (S)	416	2008	f	3/4/2008	30	Vectronic	1.50	1.00
red	SE	Skane (S)		2009			30	Vectronic	1.50	1.00
red	SE	Skane (S)	417	2008	f	3/5/2008	2	Vectronic	1.50	0.99
red	SE	Skane (S)		2009			30	Vectronic	1.50	1.00
red	SE	Skane (S)	421	2008	f	3/6/2008	30	Vectronic	1.50	1.00
red	SE	Skane (S)		2009			30	Vectronic	1.50	1.00
red	SE	Skane (S)	422	2008	f	3/7/2008	30	Vectronic	1.50	1.00
red	SE	Skane (S)		2009			30	Vectronic	1.50	1.00
red	SE	Skane (S)	423	2010	m	2/23/2010	32	Vectronic	4.00	1.00
red	SE	Skane (S)	424	2011	m	3/23/2011	32	Vectronic	4.00	1.00
red	SE	Skane (S)		2012			32	Vectronic	4.00	0.99
red	SE	Skane (S)		2013			32	Vectronic	4.00	0.99
red	SE	Skane (S)	426	2013	m	2/26/2013	32	Vectronic	6.00	0.98

red	SE	Hunneb. (SW)	427	2008	f	3/3/2008	30	Vectronic	1.50	1.00
red	SE	Hunneb. (SW)		2009			30	Vectronic	1.50	1.00
red	SE	Hunneb. (SW)	428	2008	f	2/18/2008	30	Vectronic	1.50	0.99
red	SE	Hunneb. (SW)		2009			30	Vectronic	1.50	1.00
red	SE	Hunneb. (SW)	429	2008	f	2/17/2008	30	Vectronic	1.50	1.00
red	GR	Schleswig H. (N)	444	2009	m	2/14/2009	2	Vectronic	4.00	1.00
red	GR	Schleswig H. (N)		2010			31	Vectronic	4.50	1.00
red	GR	Schleswig H. (N)	445	2009	m	3/31/2009	2	Vectronic	6.00	1.00
red	GR	Schleswig H. (N)		2010	m	3/31/2009	2	Vectronic	3.33	1.00
red	GR	Schleswig H. (N)	446	2009	f	3/28/2009	2	Vectronic	6.00	1.00
red	GR	Schleswig H. (N)		2010			30	Vectronic	3.33	1.00
red	GR	Schleswig H. (N)	448	2010	f	2/12/2010	30	Vectronic	3.50	1.00
red	GR	Schleswig H. (N)		2011			30	Vectronic	3.00	1.00
red	GR	Schleswig H. (N)		2012			30	Vectronic	4.50	1.00
red	GR	Schleswig H. (N)	449	2009	m	2/2/2009	32	Vectronic	6.00	1.00
red	GR	Schleswig H. (N)		2010			32	Vectronic	4.50	1.00
red	GR	Schleswig H. (N)	450	2008	m	3/30/2008	32	Vectronic	4.00	1.00
red	GR	Schleswig H. (N)		2009			32	Vectronic	4.00	1.00
red	GR	Schleswig H. (N)	451	2010	f			Vectronic	4.50	1.00
red	GR	Schleswig H. (N)		2011				Vectronic	3.00	1.00
red	GR	Schleswig H. (N)	452	2010	f	11/12/2009	30	Vectronic	3.33	1.00
red	GR	Schleswig H. (N)	456	2009	m	3/31/2009	2	Vectronic	6.00	1.00
red	GR	Schleswig H. (N)	457	2009	m	5/9/2009	32	Vectronic	4.00	1.00
red	GR	Schleswig H. (N)	458	2008	m	3/26/2008	32	Vectronic	6.00	1.00
red	GR	Schleswig H. (N)	459	2010	f	3/26/2010	2	Vectronic	2.00	1.00
red	GR	Schleswig H. (N)		2011			30	Vectronic	3.00	1.00
red	GR	Schleswig H. (N)		2012			30	Vectronic	4.50	1.00
red	GR	Schleswig H. (N)	460	2010	m	3/19/2010	2	Vectronic	3.33	1.00
red	GR	Schleswig H. (N)		2011			30		3.00	1.00
red	GR	Schleswig H. (N)	461	2010	f	2/27/2010	30	Vectronic	3.50	1.00
red	GR	Schleswig H. (N)		2011			30		6.00	1.00
red	GR	Schleswig H. (N)	462	2010	f	11/12/2009	30	Vectronic	3.33	1.00
red	GR	Schleswig H. (N)	463	2010	m	3/30/2010	30	Vectronic	3.33	1.00
red	GR	Schleswig H. (N)	464	2010	m	2/12/2010	31	Vectronic	3.33	1.00
red	GR	Schleswig H. (N)	465	2010	m	3/4/2010	32	Vectronic	6.00	1.00
red	GR	Schleswig H. (N)	466	2013	m	1/7/2013	30	Vectronic	3.00	1.00

APPENDIX 1. ROE DEER SUMMER HABITAT SELECTION AT MULTIPLE SPATIO-TEMPORAL SCALES IN AN ALPINE ENVIRONMENT[4]

Abstract
Habitat selection is a hierarchical process that may involve different patterns depending on the spatial and temporal scales of investigation. We studied habitat selection by European roe deer (*Capreolus capreolus*) in a very diverse environment in the Italian eastern Alps, during summer. We sampled both coarse-grained habitat variables (i.e., topographic variables, habitat types and cover) and fine-grained habitat variables (forage components of habitat) in used and available locations along the movement trajectories of 14 adult roe deer equipped with GPS telemetry collars. We used conventional logistic regression to assess roe deer habitat selection at the seasonal home range scale, and conditional logistic regression to take into account the temporal aspect of habitat selection on a weekly basis. Our results indicate that topographic variables were not significant predictors for summer roe deer habitat selection. Roe deer strongly selected dense canopy cover, probably to avoid heat stress during warm summer days. In accordance with previous observations, roe deer preferred young forest stands to climax environments, in which the dominant overstory species were ash (*Fraxinus spp.*) and hazel (*Corylus avellana*). Roe deer positively selected shrubs (in particular, *Fraxinus* spp., *Erica herbacea*, *Rhododendron* spp. and *Vaccinium* spp.) throughout the study period, whereas selection for grasses and sedges emerged only at the weekly scale. Habitat selection was clearly related to vegetation phenology, since roe deer selected plants in the most nutritive phenological stages, i.e., shrubs with buds, new leaves and fruits, and newly emergent grasses and sedges. Finally, we found stronger and more significant regression coefficients for forage components of habitat and habitat types at the weekly scale, indicating that matching spatial and temporal scales may improve our understanding of ecological patterns driving habitat selection. Conversely, selection patterns for canopy cover did not change across scales, indicating that this variable likely drives habitat selection in a similar way throughout the same season.
Keywords Alps; canopy; Capreolus capreolus; conditional logistic regression; European roe deer; GPS telemetry; spatio-temporal scale; third order habitat selection; trajectories

[4] This manuscript has been submitted to *Hysterix*. Authorship for this manuscript is Mancinelli, S., W. Peters, L. Boitani, M. Hebblewhite, F. Cagnacci

Introduction

Within Hutchinson's ecological theatre, where the evolutionary play is performed (Hutchinson 1965), the field of habitat ecology represents one of the main acts. Considering its niche-based definition, habitat is the ensemble of resources and conditions present in an area producing occupancy and determining the survival and reproduction of organisms (Hall et al. 1997, Hirzel and LeLay 2008). Habitat selection in particular is defined as the multi-scale process by which an animal chooses resources (Johnson 1980). Because habitat selection directly acts on the survival and reproductive success of individuals, it indirectly affects population dynamics and species distributions (Holt 2003, Gaillard et al. 2010). Habitat selection may be influenced by a variety of factors, such as nutrition, behavior, competition, predation, but also the scale of selection and can be recognized as a hierarchical process in space and time (Johnson 1980, Senft 1987, Wiens 1989, Manly et al. 2002, Hirzel and Le Lay 2008).

Scales in space and time have been long recognized as central themes in ecology (e.g. Hutchinson 1965, Gaillard et al. 2010). For example, the activities animals undertake to meet their needs, such as feeding, reproducing, moving, occur at different spatial scales. For the field of habitat ecology, Johnson (1980) provided an intuitive framework in which selection scales are nested. He defined the first order selection scale as the distribution range. At the second order animals should select home ranges. At the third order, resources within the home range should be selected and finally, at the fourth order scale, small site specific resources such as nests or den sites or specific foraging items should be selected. While these levels of selection are only broad categorizations along a continuum of spatial selection scales from very fine to very coarse (Gaillard et al. 2010), they provide useful guidelines for the study of habitat selection.

Next, Wiens (1989) pointed out that ecological processes are bounded by the relationships between the spatial and temporal scale of variation (i.e., processes taking place at small spatial scales will also be defined by small temporal scales). Thus, as spatial scaling increases in ecological systems, temporal scaling increases concurrently. Defining the spatial scale at which habitat selection is defined also leads to defining the temporal scale along a continuum of spatio-temporal dimensions (Gaillard et al. 2010). For example, decisions animals make at different temporal scales may include bites taken at very short time intervals within seconds, minutes or hours (Senft et al. 1987, Nathan et al. 2008). In contrast, at the spatial scale of home range occupancy intervals between decisions may last hours, days, months and years. At the broadest scale, spatio-temporal dynamics at the species level are subject to processes over hundreds of square kilometers during millions of years. While intuitive, the concept of temporal scaling has rarely been recognized and incorporated into evaluating the role of scaling in habitat selection studies, although habitat selection can be variable in time due to changes in resource quantity and quality. Mismatching space-time scaling may mask ecological relationships and average out fine-scale habitat selection patterns (Wiens et al. 1989).

The European roe deer (*Capreolus caprolus*) is one of the most common ungulate species in Europe (Melis et al. 2009), where it can occupy a diversity of habitat, including deciduous and coniferous continental forests, Mediterranean scrublands, agricultural plains, but also high latitudes and altitudes, where harsh winters and a short growing season limit population distribution and abundance (Jepsen and Topping 2004). At the latitudinal and altitudinal extremes of its distribution range, variable seasonal habitat

selection patterns including seasonal migration, allow roe deer to adapt to changes in habitat suitability in space and time (Mysterud 1999, Ramanzin et al. 2007, Cagnacci et al. 2011). However, while being a generalist species with a large fundamental niche, roe deer favor heterogeneous or mixed-habitat, providing a combination of concealment cover for protection from predators and humans and high quality forage (Duncan et al. 1998, Said and Servanty 2005, Said et al. 2005, Cederlund et al. 1998, Mysterud and Ostbye 1999). Being a small concentrate selector, roe deer generally prefer highly palatable browse vegetation, such as early phenological stages of forbs and shrubs, with high nutritional protein and low fiber contents (Demment and Van Soest 1985, Tufto et al. 1996; Gill et al. 1996). At the same time, food habits of roe deer are plastic and may change rapidly (Tixier and Duncan 1996, Cornelis et al. 1999) in response to changes in the spatial and temporal availability of food items, leading to a strong seasonal diet specialization (Duncan et al. 1998).

In general, research seems to indicate that roe deer show a high degree of ecological plasticity, but they are very selective at small microhabitat scales, such as foraging and seeking protective cover. However, most studies on fine-scale habitat composition, including forage plants, were conducted in optimal roe deer habitat, such as central Europe (e.g., Maillard et al. 1989, Jong et al. 1995) and plains (e.g., Holisova et al. 1982, 1984), or controlled conditions (Tixier et al. 1997). Unfortunately, in more extreme and highly seasonal environments at the limits of their distribution range, such as alpine regions, studies that investigate how topography, canopy and plant communities affect roe deer habitat selection are rare. Indeed, alpine environments are characterized by high heterogeneity, because habitat composition changes frequently over short distances due to, e.g., extreme gradients in elevation, aspect and slope, which condition vegetation community diversity and rapid changes in phenology. Because such heterogeneity is likely to be reflected by roe deer home ranges, the alpine environment offers a unique opportunity to study how covariates at different grain sizes may affect third order habitat selection in this small ruminant.

We aimed to study selection of habitat covariates with different grain sizes, ranging from larger grained ***macro-habitat*** covariates, such as topography or habitat class, to very fine grained ***micro-habitat*** observation units, such as plants found within sampling quadrats. Moreover, we investigated these effects at two ***temporal scales***, ***seasonal*** and ***weekly***. We outlined our objectives, hypotheses and predictions in Table 1. In general, because of their overall high ecological plasticity, but also very specialized feeding habits, we expected differing degrees of selectivity for coarse and fine grained habitat covariates (H1). First, we predicted little selectivity for coarse grained habitat variables, such as topographic covariates (P1a). Next, there is general agreement that the two major habitat requirements for roe deer are forage (Duncan et al. 1998) and cover for concealment from predators (Cederlund et al. 1998). One strategy by which roe deer may relieve heat stress and thus lower energy expenditure during summer is to use dense canopy cover for shade (e.g., Mysterud 1996). Therefore, we expected that roe deer would show positive selection for dense canopy cover (P1b). Next, because roe deer are considered concentrate selectors (Van Soest 1994), we expected their third-order habitat selection to be driven also by habitat providing highly nutritious plants. Thus, we predicted early successional habitats to be preferred, because they provide more browse and hiding cover (P1c). As roe deer show high energy and nutrient requirements and

preference for the richest parts of the consumed plant species (Tixier and Duncan 1996), we expected to find a positive selection for fine-grained microhabitat covariates indicating high-quality food resources, such as shrubs and forbs in their earlier phenological stages (P1d; Albon and Langvatn 1992, Van der Wal et al. 2000, Mysterud et al. 2001, Hebblewhite et al. 2008).

To detect patterns of environmental heterogeneity at specific spatial scales we must also match them with appropriate temporal scales within the same domain (Wiens 1989). Finding the appropriate units for both space and time remains a fundamental challenge in habitat selection studies (Gaillard et al. 2010). For our second objective, we aimed to fill this gap by comparing used versus available animal locations in a matched-case design along a temporal continuum throughout the summer season. Specifically, we hypothesized to improve our analysis for dynamic covariates when comparing used and available roe deer locations matched for the same sampling time (H2; Compton et al. 2002), rather than averaging covariates out throughout the entire summer season. In particular, we predicted to find similar selection patterns for covariates that remain fairly static throughout one summer season (macro-habitat), since these covariates are supposed to drive habitat selection in a similar way throughout the same season (P2a). Conversely, we predicted to find stronger or more significant regression coefficients for the fine-grained covariates that change throughout the summer season, e.g. forage components (P2b).

Materials and methods

Study area

The study area (approximately 40,000 ha) is located in the Italian eastern Alps in the Autonomous Province of Trento [Figure 1]. Elevation ranges from 400 m in the main valleys to 3,500 m at the highest peaks in the Brenta and the Adamello-Presanella mountain ranges and the area is characterized by a high environmental, morphological and geological complexity. Along the valley bottoms agricultural grasslands and crops as well as deciduous forests, mainly comprised by European beech (*Fagus sylvatica*) and European ash (*Fraxinus excelsior*), predominate. Understory vegetation is patchily distributed and is dominated by common hazel (*Corylus avellana*) and brambles (genus *Rubus*). Higher elevations and the narrow lateral valleys are covered by coniferous forest, mainly comprised of Norway spruce (*Picea abies*), silver fir (*Abies alba*) and European larch (*Larix decidua*). Mountain pine (*Pinus mugo*) as well as shrublands of rhododendron (genus *Rhododendron*) interspersed with alpine grasslands prevail above elevation of 1,600. Ungulate species inhabiting the region include (in order of abundance): roe deer, chamois (*Rupricapra rupricapra*), red deer (*Cervus elaphus*), and ibex (*Capra ibex*). The predator community is characterized by red foxes (*Vulpes vulpes*) and reintroduced brown bears (*Ursus arctos arctos*). The human population density of approximately 31/km² is low in comparison to other parts of Italy.

Roe deer location data

We used data from 14 radio-collared roe deer (10 females, 9 adults and 1 subadult, and 4 adult males), which were captured throughout the study area during winter of 2012/2013 using individual box traps (Schmenitz *et al.* 1994). All roe deer were fitted with Global Positioning System (GPS) collars (Vectronic Aerospace, GSM GPS Plus, Berlin, Germany). All collars were programmed to collect one location every three hours and equipped with a Global System for Mobile Communications (GSM) device, a very high-

frequency (VHF) beacon and a drop-off mechanism. All animal capture and handling procedures were approved by animal care protocols of the Trento Province (Wildlife Committee of the Autonomous Province of Trento, September 11th 2011) and the University of Montana (AUP 060-12MHWB-113012).

Sampling design

We studied fine-scale roe deer habitat selection by comparing used locations to random available locations between April and October 2013. The study time frame is ecologically important for roe deer, since it corresponds to the reproductive season, comprehending the establishment and defense of territories, natal dispersal, births and the rutting period (Linnell *et al*. 1998). Moreover, in our study area, where partial migration was observed (Ramanzin *et al.* 2007), the time interval we chose includes both the migration during spring from winter to summer ranges, as well as the start of the fall migration, from summer to winter ranges (Cagnacci *et al.* 2011). Due to an incomplete GSM coverage throughout the study area, we employed two different methods to determine used and available locations. First, for animals for which we received GPS locations via GSM network, we projected a 50 m grid over the location data of animals every eight days and selected the grid cell with the highest number of animal locations. Within this cell we selected the most recent GPS location as our used location. We *paired* each *used location* with *one random available location* in the closest cell without GPS locations. All spatial analyses were conducted in Quantum GIS (1.8.0). Next, for animals for which GSM coverage was not available, we determined used locations using VHF-triangulation once every 8 days. We recorded ≥ 3 bearings within approximately 30 min to avoid larger movements by the animal (Millspaugh *et al.* 2012). To account for VHF triangulation error, and the periodic assessment of the location, we validated roe deer presence at estimated roe deer used locations by searching for recent signs of roe deer presence, such as fresh tracks, feces and bed sites. In this case, we determined available locations in a random direction at a distance of 150 m from the used locations. As a further validation, we assessed how the presence of VHF data could have affected our sampling design. We therefore calculated a VHF error, in terms of distance (m) between a given VHF triangulation and the corresponding GPS used location which we would have sampled in presence of GSM coverage at the time of sampling. We obtained the missing GPS locations by GSM download, after animals re-entered the GSM coverage, and we matched them to the sampled VHF location. The average distance was found to be 386 m ± 302 m . Moreover, we tested for the effect of method on our predictions (see Statistical analyses below).

In used and available locations we estimated several macro-habitat covariates, including topography, habitat types, cover (Mysterud and Ostbye 1999) and micro-habitat components, i.e. vegetation composition and phenology (Hebblewhite *et al.* 2008). In particular, we recorded the macro-habitat covariates at the point location or grid cell scale, whereas we measured the micro-habitat covariates within sampling subunits (1 m^2 X 2 quadrats for vegetation; 7m^2 quarter circle for shrubs). We decided to sample shrubs, that we defined as dicotyledons with a woody stem<7 cm diameter, both in the vegetation sampling quadrats, and in an additional larger area, given the predicted importance of this highly nutritious plants/vegetative stage for roe deer (Duncan et al. 1998). For a detailed description of all habitat covariates, please see Supplementary material Appendix A.

Statistical analyses

To address our research objectives, we classified our predictor variables into three datasets: 'topography and cover' (macro-habitat), all plant composition and phenology within sampling quadrats ('plants', micro-habitat) and shrub composition and phenology within sampling quarter circles ('shrubs', micro-habitat) present at the sampling sites. All statistical analyses were conducted in R, version 3.2.0 (R Core Team 2013). Where appropriate, we transformed proportional data by an arcsin square-root transformation.

In an initial phase we conducted exploratory analyses using principal component analysis (PCA) and screening all candidate covariates for collinearity using Pearson's *r*. In case of collinear covariates we retained the covariate with the higher absolute PCA loading score (Zuur *et al* 2010) in the following modelling phase of analyses. When the number of covariates was very high (e.g., 'plants'), we also used an *a priori* criterion to select covariates relevant to test the working hypotheses. We then combined all relevant covariates to derive a full additive model for each dataset.

To estimate roe deer resource selection, we built Generalized Linear Models (GLMs; Guisan *et al.* 1999, Hosmer and Lemeshow 2000). We used conventional logistic regression (Hosmer and Lemeshow 2000) to model habitat selection by roe deer throughout the duration of the summer (Objective 1; Table 1). We also compared the likelihood of our final fixed-effects models with the same Generalized Linear Mixed Model (GLMM) including the individual animal as the sampling unit and thereby accounting for variation between individuals and uneven sample sizes (Rabe-Hesketh *et al.* 2004). We also included method to identify used locations (GPS or VHF) as random effect to test the influence of different sampling procedures on data fitting. Next, to address our second objective [Table 1], we modeled each spatially and temporally matched pair of used and available locations (see above, Sampling design) by means of conditional logistic regression (matched-case control design; Compton *et al.* 2002). We thus accounted for the temporal variation in habitat use, at a weekly scale.

We used a natural average method to obtain robust parameter estimates (Burnham and Anderson 2002). This procedure implies calculating a weighted average of parameter estimates, so that parameter estimates from models that provide little information about the variation of the response variable are given little weight (Arnold 2010). We first performed a model selection on models with all possible combinations of covariates included in the full model for each dataset by means of Akaike Information Criterion (AIC, Burnham and Anderson 2002). We then decided to retain only the top models ($\Delta AIC<2$) for the model averaging approach (MuMIn R package, Barton 2011). Moreover, when necessary we recomputed simplified best models based only on covariates with significant averaged coefficients ($p < 0.05$), for a more synthetic assessment of goodness-of-fit, and in agreement with the principle of parsimony.

Results

Six main results emerged from our study: 1) as expected, topographic variables (elevation, aspect and slope) did not emerge as significant predictors for habitat selection by roe deer (P1a); 2) as predicted, roe deer strongly selected dense canopy closure, probably to avoid heat stress during warm summer days, but contrary to our prediction, hiding cover had only a marginal effect on habitat selection (P1b); 3) as expected, roe deer preferred young forest stands with abundant understory rather than climax environments (P1c); 4) in agreement with our prediction, roe deer positively selected shrubs in the most nutritive phenological stages (especially buds and new leaves)

throughout summer (P1d); conversely, we did not find a selection for forbs in any phenological stage; 5) when looking at the weekly scale, we observed similar selection patterns (i.e., regression coefficients and their significance) for canopy cover, indicating that this variable likely drive habitat selection by roe deer in a similar way throughout the same season; conversely, regression coefficients were higher for the two preferred habitat types, *Corylus avellana* and *Fraxinus* spp., indicating a relatively stronger selection for this coarse-grained habitat variables at a weekly scale (P2a); 6) we generally found stronger regression coefficients for forage items, when matching used and available locations on a weekly scale; in particular, we observed a positive selection for newly emergent grasses and sedges at a weekly scale (P2b).

Exploratory phase and covariate selection

In the 'topography and cover' dataset [Appendix A, *Tab. A1*] we recorded the following dominant tree/shrub species during the survey: *Corylus avellana*, *Fagus sylvatica*, *Fraxinus* spp, *Picea abies*, *Pinus sylvestris*, plus open fields. As a final set of covariates, we selected aspect, elevation, canopy cover, hiding cover at 20 m, *Corylus avellana* and *Fraxinus* spp. based on the results of our exploratory analyses, i.e., PCA [Figure 2a] and correlation for subsequent resource selection function modelling. We had to exclude slope from the modeling process, because we found a positive correlation between slope and canopy cover. However, the latter had a higher PCA loading (PCA loading $_{\text{canopy cover}}$ = 0.85, PCA loading $_{\text{slope}}$ = 0.65 along the first axis). Similarly, we excluded hiding cover at 5 m, since we found a positive correlation with hiding cover at 20 m, that had a higher PCA loading (PCA loading $_{\text{hiding cover 5m}}$ = 0.13, PCA loading $_{\text{hiding cover 20m}}$ = 0.26) . Finally, we found a positive correlation between canopy cover and *Fagus sylvatica* and between elevation and *Picea abies*. We decided to exclude both habitat type covariates, based on PCA loading (PCA loading $_{\text{canopy cover}}$ = 0.85, PCA loading $_{\textit{Fagus sylvatica}}$ = 0.49; PCA loading $_{\text{elevation}}$ = 0.17, PCA loading $_{\textit{Picea abies}}$ = 0.13).

Next, we selected the covariates to formulate the full model for the 'plants' dataset. This dataset potentially included all possible combinations of plant classes and phenological stages [Appendix A, *Tab. A1*]. Therefore, besides PCA [Figure 2b], we also used *a priori* criteria based on working hypotheses to reduce the number of predictors. First, we generally found a negative correlation between new plants and old alive plants (which is understandable, given that new sprouts emerge on old alive plants). We decided to select new plants, for consistency with the working hypotheses, although old alive plants had sometimes a stronger PCA loading (PCA loading $_{\text{new forbs}}$ = 0.42, PCA loading $_{\text{old alive forbs}}$ = -0.45; PCA loading $_{\text{new shrubs}}$ = 0.38, PCA loading $_{\text{old alive shrubs}}$ = -0.59; PCA loading $_{\text{new grasses/sedges}}$ = 0.51, PCA loading $_{\text{old alive grasses/sedges}}$ = -0.47). For similar reason, i.e., coherence with the hypotheses, we decided to exclude cured plants, old dead plants, and ferns. The full model for plants therefore included: forbs, grasses/sedges and shrubs associated with two phenological stages: newly emergent (or new/old alive with new leaves referring to shrubs) and flowering/fruiting/mature.

In the 'shrubs' dataset, we recorded the following species during the survey: *Corylus avellana*, *Erica herbacea*, *Fagus sylvatica*, *Fraxinus* spp., *Picea abies*, *Rhododendron* spp., *Rubus* spp., *Vaccinium* spp [Appendix A, *Tab. A1*]. We found a positive correlation between *Corylus avellana* and *Rubus* spp. (r = 0.106), *Rhododendron* spp. and *Erica herbacea* (r = 0.190) and between *Rhododendron* spp. and *Vaccinium* spp. (r = 0.242), as shown in Figure 2c. Thus, we decided to add these shrub species in two

groups: group 1 (*Corylus avellana* + *Rubus* spp.; G1) and group 2 (*Rhododendron* spp. + *Erica herbacea* + *Vaccinium* spp.; G2). Thus, the full model for 'shrubs' included *Fraxinus* spp., group 1 and group 2 associated with two phenological stages: new/old alive with new leaves and old alive/old alive with buds.

Roe deer habitat selection at the seasonal home-range scale

For 'topography and cover', the model selection according to AIC yielded three top models with ΔAIC<2 [Appendix B, *Tab. A2a*]. Aspect was not present in any of the top models. The averaged model obtained with multi-model inference [*Tab. 2a*] confirmed our first prediction (P1a), as it did not include aspect, and indicated no significant selection for elevation. Our results also partially confirmed our second prediction (P1b), indicating that roe deer positively selected dense canopy cover, whereas hiding cover only marginally contributed to habitat selection ($\beta = 0.012$, $p = 0.077$). As expected, roe deer preferred young forest stands with abundant understory (P1c) as shown by the selection for the two shrub habitat types dominated by *Corylus avellana* and *Fraxinus* spp. The simplified best model based only on significant covariates [*Tab. 2b*] included canopy cover, *Corylus avellana* and *Fraxinus* spp. with coefficients very similar to the averaged ones. The R^2 for the simplified best model was 0.24. The addition of random effects, i.e., individual roe deer and method used to define used locations, did not improve the simplified best model fit to the data (proportion of variance explained = $1.427e^{-11}$, proportion of variance explained = $1.0e^{-12}$, respectively).

With respect to the 'plants' dataset, we obtained eight top models with ΔAIC<2 [Appendix C, *Tab. A3a*]. The averaged regression coefficients for this dataset (*Tab. 2a*) confirmed our prediction (P1d), indicating that roe deer positively selected shrubs in the most nutritive phenological stages throughout summer, especially with new emerging leaves. Shrubs with flowers and fruits only marginally contributed to habitat selection ($\beta = 0.200$, $p = 0.072$). All other averaged coefficients were not significant, and especially we did not find a selection for forbs in any phenological stage, contrary to what expected (P1d). The simplified best model based on significant averaged coefficients [*Tab. 2b*] included only one covariate, i.e., new/old alive with new leaves shrubs ($\beta = 0.094$, $p = 0.007$). The simplified best model had a $R^2 = 0.50$. The addition of random effects, i.e., individual roe deer and method used to define used locations, did not improve the simplified best model fit to the data (proportion of variance explained = $1.0e^{-12}$ for both random effects).

Lastly, for the 'shrubs' dataset, we obtained for top models [Appendix D, Table A4a]. The averaged regression coefficients [*Tab. 2a*] further highlighted that the most nutritive phenological stages (i.e., buds and new leaves) of shrubs are strongly selected by roe deer during summer (P1d). In particular, roe deer in our study area mainly selected four shrub species: *Fraxinus* spp., which can be mainly found in the valley bottoms, and three species (group G2: *Erica herbacea*, *Rhododendron* spp. and *Vaccinium* spp.) which generally represent a vegetation community characteristic of higher altitudes. Other phenological stages presented not significant coefficients. The simplified best model [*Tab. 2b*] thus included new/new leaves *Fraxinus* spp., new/new leaves group 2 and old alive/buds group 2, with an $R^2 = 0.24$. The addition of random effects, i.e., individual roe deer and method used to define used locations, did not improve the best model fit to the data (proportion of variance explained = $1.427e^{-11}$, proportion of variance explained = $1.0e^{-12}$, respectively).

Roe deer habitat selection at the spatially and temporally matched scale

The conditional logistics model selection for 'topography and cover' provided the same top models obtained in the conventional logistic regression analysis [Appendix B, *Tab. A2b*]. The averaged regression coefficients [*Tab. 3a*] confirmed our predictions, as we observed at weekly scale similar selection patterns than at seasonal scale for canopy cover ($\beta_{log} = 0.041$, $p < 0.001$; $\beta_{c\text{-}log} = 0.050$, $p < 0.001$), indicating that this variable likely drive habitat selection by roe deer in a similar way during the same season (P2a). Conversely, regression coefficients for the two habitat types were higher at the weekly scale than at the seasonal scale, (*Corylus avellana*: $\beta_{log} = 1.069$, $p = 0.003$ vs $\beta_{c\text{-}log} = 1.800$, $p = 0.001$; *Fraxinus* spp.: $\beta_{log} = 1.205$, $p = 0.002$ vs $\beta_{c\text{-}log} = 1.550$, $p = 0.007$), indicating a relatively stronger selection for this coarse-grained habitat variables at a weekly scale (P2a). The simplified best model based only on significant averaged coefficients [*Tab. 3b*] included canopy cover, *Corylus avellana* and *Fraxinus* spp., with $R^2 = 0.30$.

The conditional logistics model selection for 'plants' provided three top models [Appendix C, *Tab. A3b*]. The corresponding averaged coefficients [*Tab. 3a*] for new/new leaves shrubs was higher at the weekly scale than at the seasonal scale (P2b; $\beta_{log} = 0.091$, $p = 0.013$ vs $\beta_{c\text{-}log} = 0.124$, $p = 0.004$). Moreover, newly emergent grasses/sedges were also positively selected at a weekly scale ($\beta = 0.105$, $p = 0.044$), whereas this covariate was not included in the seasonal averaged model. Flowering, fruiting and mature forbs and shrubs and newly emergent forbs were marginally, or not significant. The simplified best model based on significant averaged coefficients [*Tab. 3b*] only included new/ new leaves shrubs and newly emergent grasses/sedges, with $R^2 = 0.48$.

Lastly, the top models for selection of 'shrubs' at the weekly scale [Appendix D, *Tab. A4b*] provided the same results than those obtained with conventional logistic regression at the seasonal scale. The averaged model [*Tab. 3a*] indicated a positive selection for new/new leaves *Fraxinus* spp., new/new leaves group 2 and old alive/buds group 2. The other covariates had not significant averaged coefficients. According to our prediction (P2b), the averaged coefficients suggested a stronger selection at the weekly scale than at the seasonal scale, for all classes included (new/new leaves *Fraxinus* spp.: $\beta_{log} = 0.254$, $p < 0.001$ vs $\beta_{c\text{-}log} = 0.283$, $p < 0.001$; new/new leaves group 2: $\beta_{log} = 0.101$, $p = 0.011$ vs $\beta_{c\text{-}log} = 0.128$, $p = 0.008$; old alive/buds group 2: $\beta_{log} = 0.277$, $p = 0.023$ vs $\beta_{c\text{-}log} = 0.321$; $p = 0.031$). The simplified best model included the same covariates, with $R^2 = 0.31$ [*Tab. 3b*].

Discussion

Roe deer habitat selection at the seasonal home-range scale

Using an individual-based approach, we assessed habitat selection by roe deer in a very diverse environment in the Italian Alps during summer. The environmental heterogeneity that characterizes the study area allowed us to match coarse grained habitat variables, such as topography and cover, and fine grained habitat variables, such as food items, in a comprehensive analysis of third-order habitat selection in this small ungulate. The presence of a high ecological plasticity was expected from previous research (e.g., Jepsen and Topping 2004) and was further confirmed by our results. Indeed, roe deer in our study area occupied a wide altitudinal range from 457 m to 1.916 m a.s.l. Moreover, roe deer were found not to select habitat with respect to aspect but preferred habitat diversity. Aspect is generally regarded as a topographic covariate involved in habitat selection by

temperate ungulates given its effect on food resources availability and quality. For example, Albon and Langvatn (1992) reported that the protein content of grasses and herbs was higher on north-facing slopes compared with south-facing slopes during spring in Norway. However, Mysterud et al. (2001) found that body weight of migratory red deer (*Cervus elaphus*) was positively correlated with access to diversity of aspects and variable topography rather than with the availability of a particular aspect or altitudinal class in Norway. Our results are consistent to these findings and may be related to the rapid changing in aspect gradients that characterizes our study area. Interestingly, roe deer used more steep areas over gently sloping areas, since the average value for this variable was 25.3° (±12°). Parker et al. (1984) found that in mule deer and elk the costs of locomotion increase as a function of increasing slope. Moreover, Thomas and Hobbs (1989) observed that energy expended by bighorn sheep and mountain goats for lifting 1 kg of body weight one vertical meter on a 21.5° slope exceeded the highest cost documented for quadrupeds. Thus, the costs of locomotion for roe deer in steep alpine terrains may be high. Nevertheless, our results are not consistent with these considerations and may be related to 1) the fact that roe deer are not cursorial ungulates but agile jumpers; 2) their small body size, which may lower their costs for locomotion in steep areas (Parker et al. 1984) and/or 3) the strong positive correlation we found between slope and canopy cover.

Canopy cover emerged as a strong driver of summer habitat selection by roe deer amongst macro-habitat covariates. Numerous studies have documented how cervids selectively use canopy cover to avoid adverse weather conditions, including studies on white-tailed deer (*Odocoileus virginianus*, Gates and Harmann 1980), mule deer (*Odocoileus hemionus*, e.g., Wood 1988), red deer (*Cervus elaphus*, Staines 1976), moose (*Alces alces*, e.g., Demarchi and Bunnell 1995) and roe deer (*Capreolus capreolus*, e.g., Mysterud and Ostbye 1995, Mysterud 1998). Use of canopy cover relates to extreme temperatures, radiation and wind speed (Mysterud and Ostbye 1999). As our study was conducted during spring and summer, roe deer probably selected dense canopy cover to lower energy expenditures due to heat stress. Similarly, Mysterud (1996) observed that roe deer prefer to bed down below dense canopy cover during warm summer days in southern Norway. Whereas use of canopy cover mainly relates to thermoregulation, hiding cover is usually connected to predation risk, that in our study area is low. Indeed, the predator community is characterized by red foxes (*Vulpes vulpes*), that have been reported to prey mainly on roe deer fawns during the first two months of life (Aanes et at. 1998) and reintroduced brown bears (*Ursus arctos arctos*) at low densities, that is been shown to rarely prey on roe deer, also in the study area (Frassoni 2002). Even if Tufto et al. (1996) observed that roe deer continue to prefer habitat with high concealment cover also in the absence of predators, our results show that hiding cover marginally contributed to roe deer habitat selection in our study. One hypothesis to explain such observation is that forest habitat characteristic of our study area provide a lower perception of risk per se than open habitat, due to lower visibility, and the possibility to quickly escape for an agile species such as roe deer (Mysterud and Ostbye 1999). Further, other research showed that roe deer in open areas have a very high vigilance, and compensate the high visibility with specific tactics**,** such as grouping behavior (Mrlik 1991, Gerard et al. 1995, Bonnot et al. 2014).

Structural components of habitats, such as canopy and the habitat type, are likely to affect both food quality and cover availability (Said et al. 2005). Being an ecotonal species generally related to early successional habitats, roe deer in our study population strongly preferred two habitat types, which were dominated by two understory species, hazel (*Corylus avellana*) and ash (*Fraxinus* spp.). These species are generally found in young forest stands in the alpine environment, before being replaced by beech (*Fagus sylvatica*) or spruce (*Picea abies*) forests (Bernetti 1995), and can develop dense patches of woodland thanks to their high vegetative regeneration rate. These thick habitats provide an optimal combination of high quality forage and concealment cover, and can therefore optimize the food and cover trade-off in this small concentrate selector.

Since roe deer are herbivores, the selection for a particular habitat type is expected to reflect foraging strategies and thus to overlap with the selection of feeding sites (e.g., Andersen et al. 1998, Pettorelli et al. 2001). Indeed, our results of shrub-habitat selection may be suggestive for the selection of shrubs as potentially major foraging items throughout summer. In particular, roe deer selected for habitat patches rich in *Fraxinus* spp., *Erica herbacea*, *Rhododendron* spp. and *Vaccinium* spp. The selection for *Rhododendron* spp. is remarkable, since it is generally considered a toxic plant. However, Mussa et al. (2003) already found this shrub species in the summer diet of roe deer in an Alpine environment, by means of faecal analysis method. To be noticed, roe deer are able to use plants which are protected by chemical defenses (Duncan et al. 1998), so that might be the case for rhododendron too. Alternatively, the selection for rhododendron might be a consequence of its association with other forage species, such as bilberry (*Vaccinium myrtillus*), which has been reported to be one of the main food resources selected by roe deer in Norway during winter (Mysterud et al. 1997). As expected, shrubs were selected in the most nutritive phenological stages, i.e., buds and new leaves. We did not find a selection for forbs, although roe deer are generally known to feed on them, especially during spring and summer (e.g., Mysterud 1996). The strong selection for shrubs and absence of selection for forbs are in contrast with what reported by Mussa et al. (2003), who found that the summer diet of roe in the western Alps was mainly composed by herbaceous species (dicotyledons) and to a lesser extent by tree or shrub leaves. In general, reviews of studies of roe deer feeding habits (Tixier and Duncan 1996, Cornelis et al. 1999, Gebert and Verheyden-Tixier 2001) revealed that its diet composition is mainly explained by the environments in which they forage (Duncan et al. 1998). Thus, conclusions about food selection drawn in a particular study area will rarely be relevant to other areas (Storms et al. 2008). Furthermore, while we did not assess diet composition through direct observations or fecal analysis, i.e., 4th order habitat selection, our findings further support roe deer dependence on specific plant typology and phenology stages, which can be explained by the comparatively high nutritional requirements of this small browser with low fat storages in general (Duncan et al. 1998).

Roe deer habitat selection at the spatially and temporally matched scale

By analyzing the same datasets with two different statistical approaches, i.e. conventional and conditional logistic regression, we assessed the presence of temporal variation in third-order habitat selection by roe deer during summer. The choice to use a multiple-scale approach in habitat selection studies is a central issue, since habitat selection patterns are not necessarily congruent across spatial and temporal scales (Morin et al. 2005). The positive selection for newly emergent grasses and sedges we observed at the

weekly scale, but not at the seasonal home range scale, is an example of how mismatching space-time relationships may mask fine-scale habitat selection patterns. Our result is consistent with what observed by Cornelis et al. (1999), which found that during spring and summer roe deer can double their exploitation of the graminoids typical of open pastures compared to the annual average.

Spatio-temporal heterogeneity of trade-offs between different limiting factors will shape habitat selection decision by individual animals and populations (Gaillard et al. 2011). According to classical theories of foraging [e.g., optimal foraging theory (Charnov 1976) and habitat selection (Rosenzweig 1981)], animals are supposed to spend most time in those habitats richest in food, and habitat selection is expected to reflect food availability (Mysterud et al. 1999). However, it is then implicitly assumed that there is no trade-off between feeding sites selection and other ecological processes, such as predator avoidance and intra- and inter-specific competition that instead may be important determinants of habitat selection. In particular, the effect of some of these additional elements might emerge at a one specific scale of analysis, thus originating differential habitat selection patterns at different temporal and spatial scales (De Cesare et al. 2013). For large herbivores, selection is commonly driven by the balance between forage quantity and quality and the presence of cover that decreases predation risk and offers protection from adverse weather conditions (Fryxell et al. 1988, Mysterud and Ostbye 1999, Rettie and Messier 2000). It is generally hypothesized that ungulates respond to 'risk-forage' trade-offs in a hierarchical fashion (Senft et al. 1987), and may select habitats that reduce risk of predation at coarser scales and maximize forage intake at smaller scales (Rettie and Messier 2000, Johnson et al. 2001, Hebblewhite and Merrill 2009). Therefore, these trade-offs should be assessed at different spatio-temporal scales. In our study area, where the predation risk is low, intra- and inter-specific competition likely represent the most limiting factors for roe deer habitat selection. The positive selection for newly emergent grasses and sedges we observed only at a weekly scale might be the result of micro-site selection to avoid competition with sympatric competing species, e.g., red deer (*Cervus elaphus*). Besides inter-specific competition, intra-specific competition and population density represent other factors affecting habitat selection (Fretwell and Lucas 1970, Fretwell 1972). For example, Kie and Bowyer (1999) found that in white-tailed deer females with young made a greater use than males of chaparral-mixed grass habitats with dense canopy cover at moderate densities, whereas at high densities males that otherwise used more open habitats increased their use of the chaparral-mixed grass as levels of intra-specific competition increased.

Another expected consequence of the analysis based on a 'paired design' are stronger covariate effects. Indeed, regression coefficients for food items in our models were higher when using conditional logistic regression. On the one side, a matched analysis does not 'average out' effects across a wide temporal scale. In particular, though, the increased coefficients for dynamic micro-habitat variables we observed may reflect the temporal variation in availability of those components. This may be particularly evident during spring and summer, when temperate ungulates are supposed to follow the 'green wave' of the vegetation phenological cycle (Bischof et al. 2012). For example, flowering/fruiting/mature shrubs only marginally affected roe deer habitat selection in the matched-paired design (Table A3d). The marginal significance of this covariate, that refers to phenological stages with highly nutritious portions of the plants (flowers and

fruits), might be due to the fact that the flowering and fruiting phases of vegetation phenology are shorter compared to the longer leaf-growth stage. Lastly, the temporal variation in habitat selection patterns we observed for some micro-habitat variables did not emerge when referring to certain macro-habitat variables, such as canopy cover, but it did for specific habitat types, such as forest with dominant ash and hazel, also providing browsing availability. Overall, our findings highlighted the importance of considering the spatio-temporal resolution in habitat selection studies to define dynamic habitat selection drivers (e.g., plant phenology), especially when habitat covariates are collected at fine spatial scales. Roe deer represented a perfect case study for such approach, thanks to their well-established 'picky' nature when selecting micro-habitat components (e.g., food items).

Conclusions

Our results partially confirmed early observations on roe deer habitat selection, by using state-of-the-art habitat selection techniques. In particular, we highlighted the dependence on specific plant typology and phenology stages, which can be explained by the comparatively high nutritional requirements of this small browser with low fat storages (Duncan et al. 1998).

Despite its high ecological plasticity with respect to coarse-grained habitat variables, roe deer might be directly affected by the alteration of fine-grained habitat characteristics, such as the availability of high-quality forage. Land use practices (esp. forest management of mature forests) and the variation of the vegetation growing season due to climate change are therefore potential factors affecting future distribution and abundance of roe deer throughout Europe. For example, a range contraction could be expected at the southern end of the distribution due to the increasing frequency of prolonged drought periods. In contrast, an expansion might be possible at northern latitudes or at intermediate altitudes in the alpine range due to lower snow depths and shorter duration of snow cover, and therefore earlier and prolonged vegetation growing season (e.g., Mysterud and Sæther 2011). Future studies might for example assess the effect of likely future changes in vegetation communities in mountainous areas, which are already considered sub-optimal environments for this species.

References

Aanes, R. et al. 1998. Roe deer as prey. In: Andersen, R., Duncan, P. and Linnell, J. D. C. (Eds..) The European roe deer: the biology of success. Scandinavian University Press, pp. 139-157.

Albon, S. D. and Langvatn, R. 1992. Plant phenology and the benefits of migration in a temperate ungulate. Oikos 65: 502-513.

Andersen, R. et al. 1998. Variation in life-history parameters. In: Andersen, R., Duncan, P. and Linnell, J. D. C. (Eds..) The European roe deer: the biology of success. Scandinavian University Press, pp. 285-306.

Arnold, T. W. 2010. Uninformative Parameters and Model Selection Using Akaike's Information Criterion. J. Wildl. Manage. 74(6): 1175-1178.

Barton, K. 2011. MuMIn: Multi-model inference. R package version 1.9.5.

Bernetti, G. 1995. Selvicoltura speciale. Unione Tipografico-Eds.itrice Torinese.

Bischof, R. et al. 2012. A Migratory Northern Ungulate in the Pursuit of Spring: Jumping or Surfing the Green Wave? Am. Nat. 180(4): 407-424.

Bonnot, N. et al. 2014. Inter-individual variability in habitat use: evidence for a risk management syndrome in roe deer? Behav. Ecol. 00(00): 1-10.
Burnham, K. P. and Anderson, C. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer.
Cagnacci, F. et al. 2011. Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determinEds. by ecological factors. Oikos 120: 1790-1802.
Cederlund, G. et al. 1998. Managing roe deer and their impact on the environment: maximising the net benefits to society. In: Andersen, R., Duncan, P. and Linnell, J. D. C. (Eds..) The European roe deer: the biology of success. Scandinavian University Press, pp. 337-372.
Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. Theor. Popul. Biol. 9: 129-136.
Compton, B. et al. 2002. Habitat selection by wood turtles (*Clemmys insculpta*): an application of pairEds. logistic regression. Ecology 83(3): 833-843.
Cornelis, J. et al. 1999. Impact of season, habitat and research techniques on diet composition of roe deer (*Capreolus capreolus*): a review. J. Zool. (London) 248: 195-207.
De Cesare, N. J. et al. 2013. Linking habitat selection and prEds.ation risk to spatial variation in survival. J. Anim. Ecol. 83(2): 343-352.
Demarchi, M. W. and Bunnell, E. L. 1995. Forest cover selection and activity of cow moose in summer. Acta Theriol. 40: 23-36.
Demment, M. W. and van Soest, P. J. 1985. A nutritional explanation for body-size patterns of ruminant and non-ruminant herbivores. Am. Nat. 125: 641-672.
Duncan, P. et al. 1998. FeEds.ing strategies and the physiology of digestion in roe deer. In: Andersen, R., Duncan, P. and Linnell, J. D. C. (Eds..) The European roe deer: the biology of success. Scandinavian University Press, pp. 91-116.
Frassoni P. 2002. L'alimentazione dell'orso bruno (*Ursus Arctos*, Linneo 1758) del Trentino, nell'ambito del progetto di reintroduzione "Life Ursus" Tesi di Laurea.
Fretwell, S. D. 1972. Populations in a seasonal environment. Princeton Univ. Press.
Fretwell, S. D. and Lucas H. L. Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheor. 14: 16-36.
Fryxell, J. et al. 1988. Why are migratory ungulates so abundant? Am. Nat. 131(6): 781-798.
Gaillard, J. et al. 2010. Habitat-performance relationships: finding the right metric at a given spatial scale. Philos. Trans. R. Soc. B 365: 2255-2265.
Gates, J. E. and Harmann, D. M. 1980. White-tailEds. deer wintering area in a hemlock-northern hardwood forest. Can. Field Nat. 94: 259-268.
Gebert, C. and Verheyden-Tixier, H. 2001. Variations of diet composition of rEds. deer (*Cervus elaphus* L.) in Europe. Mamm. Rev. 31: 189-201.
Gerard, J. F. et al. 1995. Large group formation in European roe deer: an adaptive feature? Revue d'Ecologie Terre Vie 50: 391-401.
Gill, R. M. A. et al. 1996. Changes in roe deer (*Capreolus capreolus*) population density in response to forest habitat succession. For. Ecol. Manage. 88: 31-41.
Guisan, A. et al. 1998. PrEds.icting the potential distribution of plant species in an alpine environment. J. Veg. Sci. 9(1): 65-74.

Hall, L. S. et al. 1997. The habitat concept and a plea for standard terminology. Wildl. Soc. Bull. 25: 173-182.
Hebblewhite, M. and Merrill, E. 2008. Modelling wildlife-human relationships for social species with mixEds.-effects resource selection models. J. Appl. Ecol. 45: 834-844.
Hebblewhite, M., and Merrill, E. H. 2009. Trade-offs between prEds.ation risk and forage differ between migrant strategies in a migratory ungulate. Ecology 90(12): 3445-3454.
Hirzel, A. H. and Le Lay, G. 2008. Habitat suitability modelling and niche theory. J. Appl. Ecol. 45: 1372-1381.
Holisova, V et al. 1982. The winter diet of roe deer (*Capreolus capreolus*) in the southern Moravian agricultural landscape. Folia Zool. 31: 209-225.
Holisova, V. et al. 1984. The summer diet of field roe bucks (*Capreolus capreolus*) in southern Moravia. Folia Zool. 33: 193-208.
Holt, R. D. 2003. On the evolutionary ecology of species' ranges. Evol. Ecol. Res. 5: 159-178.
Hosmer, D. W. and Lemeshow, S. 2000. AppliEds. Logistic Regression. John Wiley and Sons.
Hutchinson, G. E. 1965. The Ecological Theater and the Evolutionary Play. Yale Univ. Press.
Jepsen, J. U. and Topping, C. J. 2004. Modelling roe deer (*Capreolus capreolus*) in a gradient of forest fragmentation: behavioural plasticity and choice of cover. Can. J. Zool. 82: 1528-1541.
Johnson, D. H. 1980. The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. Ecology 61(1): 65-71.
Jong, C. B. et al. 1995. Diet selection by roe deer *Capreolus capreolus* in Kielder Forest in relation to plant cover. For. Ecol. Manage. 79: 91-97.
Kie, J. G. and Bowyer, R. T. 1999. Sexual segregation in white-tailEds. deer: density-dependent changes in use of space, habitat selection and dietary niche. J. Mamm. 80(3): 1004-1020.
Linnell, J. D. C. et al. 1998. The European roe deer: A portrait of a successful species. In: Andersen, R., Duncan, P. and Linnell, J. D. C. (Eds..), The European roe deer: the biology of success. Scandinavian University Press, pp. 11-21.
Maillard, D. et al. 1989. Le regime alimentaire estival du chevreuil dans une hetraie calcicole, determine par l'analyse des contenus stomacaux. B. M. O. N. C. 139: 29-32.
Manly, B. F. J. et al. 2002. Resource selection by animals: statistical design and analysis for field studies. Chapman & Hall, London.
Melis, C. et al. 2009. PrEds.ation has a greater impact in less productive environments: variation in roe deer, *Capreolus capreolus*, population density across Europe. Glob. Ecol. Biogeogr. 18: 724-734.
Millspaugh, J. et al. 2012. Wildlife Radiotelemetry and Remote Monitoring. In: Silvy, N. J. (Eds..), The Wildlife Techniques Manual - Management (Volume 2, 7th Eds.ition). The Johns Hopkins University Press, pp. 258-283.
Morin, P. et al. 2005. Hierarchical habitat selection by North American porcupines in southern boreal forest. Can. J. Zool. 83: 1333-1342.

Mrlik, V. 1991. Active protective behaviour of roe deer (*Capreolus capreolus*) in an open habitat during the winter season. Folia Zool. 40: 13-24.

Mussa, P. et al. 2003. Preliminary study on the feEds.ing habits of roe deer (*Capreolus capreolus*) in the western Alps. J. Anim. Physiol. Anim. Nutr. 87: 105-108.

Mysterud, A. 1996. BEds.-site selection by adult roe deer *Capreolus capreolus* in southeastern Norway during summer. Wildl. Biol. 2: 101-106.

Mysterud, A. 1998. Habitat selection by roe deer relative to resource distribution and spatio-temporal scale. Dissertation, Univ. of Oslo.

Mysterud, A. 1999. Seasonal migration pattern and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway. J. Zool. (London) 247: 479-486.

Mysterud, A. and Ostbye, E. 1995. BEds.-Site Selection by European Roe Deer (*Capreolus Capreolus*) in Southern Norway during winter. Can. J. Zool. 73: 924-932.

Mysterud, A. and Ostbye, E. 1999. Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. Wildl. Soc. Bull. 27(2): 385-394.

Mysterud, A. and Sæther, B. E. 2011. Climate change and implications for the future distribution and management of ungulates in Europe. In: Putman, R., Apollonio, M. and Andersen R. (Eds..) Ungulate management in Europe. Problems and practices. Cambridge University Press, pp. 349-375.

Mysterud, A. et al. 1997. Effects of snow depth on food and habitat selection by roe deer *Capreolus capreolus* in an altitudinal gradient in south-central Norway. Wildl. Biol. 3: 27-33.

Mysterud, A. et al. 1999. Habitat selection by roe deer and sheep: does habitat ranking reflect resource availability? Can. J. Zool. 77: 776-783.

Mysterud, A. et al. 2001. Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. J. of Anim. Ecol. 70: 915-923.

Nathan, R. et al. 2008. A movement ecology paradigm for unifying organismal movement research. Proc. Natl. Acad. Sci. U.S.A. 105(49): 19052-19059.

Parker, K. L. et al. 1984. Energy expenditures for locomotion by mule deer and elk. J. Wildl. Manage. 48(2): 474-488.

Pettorelli, N. et al. 2001. Population density and small-scale variation in habitat quality affect phenotypic quality in roe deer. Oecologia 128(3): 400-405.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Rabe-Hesketh, S. et al. 2004. GeneralizEds. multilevel structural equation modeling. Psychometrika 69: 167-190.

Ramanzin, M. et al. 2007. Seasonal migration and home range of roe deer (*Capreolus capreolus*) in the Italian eastern Alps. Can. J. Zool. 85: 280-289.

Rettie, W. J. and Messier, F. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography 23: 466-478.

Rosenzweig, M. L. 1981. A theory of habitat selection. Ecology 62(2): 327-335.

Said, S. and Servanty, S. 2005. The influence of landscape structure on female roe deer home-range size. Landsc. Ecol. 20: 1003-1012.

Said, S. et al. 2005. Ecological correlates of home-range size in spring–summer for female roe deer (*Capreolus capreolus*) in a deciduous woodland. J. Zool. (London) 267: 301-308.

Schemnitz, S. D. 1994. Capturing and handling wild animals. In: Bookhout, T. A. (Eds..), Research and management techniques for wildlife and habitats. The Wildlife Society, pp. 370-418.

Senft, R. L. et al. 1987. Large Herbivore Foraging and Ecological Hierarchies. BioScience 37(11): 789-799.

Skalski, J. R. et al. 1993. Testing the significance of individual- and cohort-level covariates in animal survival studies. In: Lebreton, J-D. and North, P. M. (Eds..), MarkEds. individuals in the study of bird population, pp. 9-28.

Staines, B. W. 1976. The use of natural shelter by rEds. deer (*Cervus elaphus*) in relation to weather in north-east Scotland. J. Zool. 18: 1-8.

Storms, D. et al. 2008. Seasonal variation in diet composition and similarity of sympatric rEds. deer *Cervus elaphus* and roe deer *Capreolus capreolus*. Wildl. Biol. 14(2): 237-250.

Thomas, V. D. and Hobbs, N. T. 1989. Travel in alpine terrain: energy expenditures for locomotion by mountain goats and bighorn sheep. Can. J. Zool. 67(10): 2368-2375.

Tixier, H. and Duncan, P. 1996. Are European roe deer browsers? A review of variations in the composition of their diets. Revue d'Ecologie Terre Vie 51: 3-17.

Tixier, H. et al. 1997. Food selection by European roe deer (*Capreolus capreolus*): effects of plant chemistry, and consequences for the nutritional value of their diets. J. Zool. (London) 242(2): 229-245.

Tufto, J. et al. 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. J. Anim. Ecol. 65: 715-724.

Van der Wal, R. et al. 2000. Trading forage quality for quantity? Plant phenology and patch choice by Svalbard reindeer. Oecologia 123: 108-155.

Van Soest, P. 1994. The nutritional ecology of the ruminant. O&B Books Inc. Corvallis, Oregon.

Wiens, J. A. 1989. Spatial Scaling in Ecology. Funct. Ecol. 3(4): 385-397.

Wood, A. K. 1988. Use of shelter by mule deer during winter. Prairie Nat. 20: 15-22.

Zuur, A. F. et al. 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1: 3-14.

Table 1. Objectives, hypotheses and predictions for summer habitat selection by roe deer, *Capreolus capreolus*, in Italian eastern Alps (Autonomous Province of Trento).

Objectives	**Hypotheses**	**Predictions**
1) Roe deer habitat selection at the ***seasonal*** home-range scale	H1: Roe deer show a high ecological plasticity for coarse grained habitat covariates, but selectivity increases in response to specific requirements and for finer grained micro-habitat covariates, such as forage items	P1a: Topographic variables (macro-habitat), such as elevation, aspect and slope, will not be significant predictors for roe deer habitat selection. P1b: Roe deer will use habitat according to its cover value (macro-habitat). In particular, roe deer will select for increased canopy closure and hiding cover (horizontal and vertical cover). P1c: Roe deer will use habitat according to its overall browsing value (macro-habitat). In particular, roe deer will use habitats with higher browse availability (i.e., shrubs) and early successional forest stages (such as shrub-habitats). P1d: Finer grained (micro-habitat) variables will be selected, according to their forage quality value. Roe deer will select for areas rich in forbs and shrubs in early phonological stages.
2) Roe deer habitat selection at the spatially and temporally matched (***weekly***) scale	H2: Matching the domain of spatial and temporal scaling will improve our understanding of ecological patterns	P2a: Selection patterns for topographic covariates, habitat classes and cover (macro-habitat) will be similar to those observed at the seasonal home range scale, since these covariates are expected to drive habitat selection in a similar way throughout the same season. P2b: Regression coefficients for forage items (micro-habitat) will be stronger and more significant when matching used and available locations on a temporally (i.e., on a weekly) scale.

Table 2 (a) Model averaged coefficients and standard errors of the covariates included in the top models retained by means of AIC model selection (see Supplementary material) for seasonal habitat selection by roe deer. The predictor's weight and P-value of each term are provided. Models were obtained using conventional logistic regression. *(b)* Coefficients and standard errors of the covariates of a simplified version of the best model; n = new, nln = new/old alice with new leaves, ffm = flowering/fruiting/mature, olb = old alive/old alive with buds, G1 = *Corylus avellana* + *Rubus* spp., G2 = *Erica herbacea* + *Rhododendron* spp. + *Vaccinium* spp.

(a) Model averaging				
Covariate	**Regression Coefficient**	**Std. Error**	**P-value**	**Pred. weight**
Topography and cover				
Canopy cover	*0.041*	*0.011*	*< 0.001*	*1*
Corylus avellana	*1.069*	*0.357*	*0.003*	*1*
Fraxinus spp.	*1.205*	*0.393*	*0.002*	*1*
Hiding cover at 20 m	0.012	0.007	0.077	0.75
Elevation	$3 \cdot 10^{-4}$	$2 \cdot 10^{-4}$	0.284	0.29
Plants				
Shrub_nln	*0.091*	*0.036*	*0.013*	*1*
Shub_ffm	0.199	0.111	0.072	0.80
Grass_n	0.055	0.044	0.210	0.38
Grass_ffm	0.029	0.080	0.712	0.09
Forb_n	0.003	0.051	0.950	0.08
Forb_ffm	-0.068	0.067	0.313	0.24
Shrubs				
Fraxinus_nln	*0.255*	*0.063*	*< 0.001*	*1*
*Fraxinus*_olb	0.194	0.251	0.441	0.21
G1_nln	0.037	0.052	0.476	0.19
G1_olb	0.091	0.134	0.490	0.19
G2_nln	*1.101*	*0.040*	*0.011*	*1*
G2_olb	*0.277*	*0.121*	*0.023*	*1*
(b) Simplified best models				
Topography and cover				
Canopy cover	0.042	0.011	< 0.001	
Corylus avellana	1.095	0.355	0.002	
Fraxinus spp.	1.204	0.391	0.002	
Plants				
Shrub_nln	0.094	0.035	0.007	
Shrubs				
Fraxinus_nln	0.255	0.063	< 0.001	
G2_nln	0.101	0.040	0.011	
G2_olb	0.276	0.122	0.023	

Table 3 (a) Model averaged coefficients and standard errors of the covariates included in the top models retained by means of AIC model selection for weekly habitat selection of roe deer (see Supplementary material). The predictor's weight and P-value of each term are provided. Models were obtained using conditional logistic regression. *(b)* Coefficients and standard errors of the covariates of a simplified version of the best model; n = new, nln = new/old alice with new leaves, ffm = flowering/fruiting/mature, olb = old alive/old alive with buds, G1 = *Corylus avellana* + *Rubus* spp., G2 = *Erica herbacea* + *Rhododendron* spp. + *Vaccinium* spp.

(a) Model averaging				
Covariate	**Regression Coefficient**	**Std. Error**	**P-value**	**Pred. weight**
Topography and cover				
Canopy cover	*0.045*	*0.015*	*< 0.001*	*1*
Corylus avellana	*1.780*	*0.560*	*0.001*	*1*
Fraxinus spp.	*1.547*	*0.568*	*0.006*	*1*
Hiding cover at 20 m	0.013	0.007	0.065	0.76
Elevation	-0.003	0.003	0.374	0.27
Plants				
Shrub_nln	*0.124*	*0.042*	*0.003*	*1*
Shrub_ffm	0.211	0.112	0.060	0.80
Grass_n	*0.105*	*0.052*	*0.044*	*1*
Forb_ffm	-0.090	0.072	0.214	0.35
Shrubs				
Fraxinus_nln	*0.283*	*0.074*	*< 0.001*	*1*
*Fraxinus*_olb	0.148	0.251	0.556	0.19
G1_nln	0.017	0.052	0.743	0.17
G1_olb	0.093	0.140	0.505	0.20
G2_nln	*0.128*	*0.049*	*0.009*	*1*
G2_olb	*0.321*	*0.147*	*0.031*	*1*
(b) Simplified best models				
Topography and cover				
Canopy cover	0.050		< 0.001	
Corylus avellana	1.831		0.001	
Fraxinus spp.	1.563		0.006	
Plants				
Shrub_nln	0.124		0.003	
Grass_n	0.104		0.046	
Shrubs				
Fraxinus_nln	0.283		< 0.001	
G2_nln	0.128		0.008	
G2_olb	0.390		0.032	

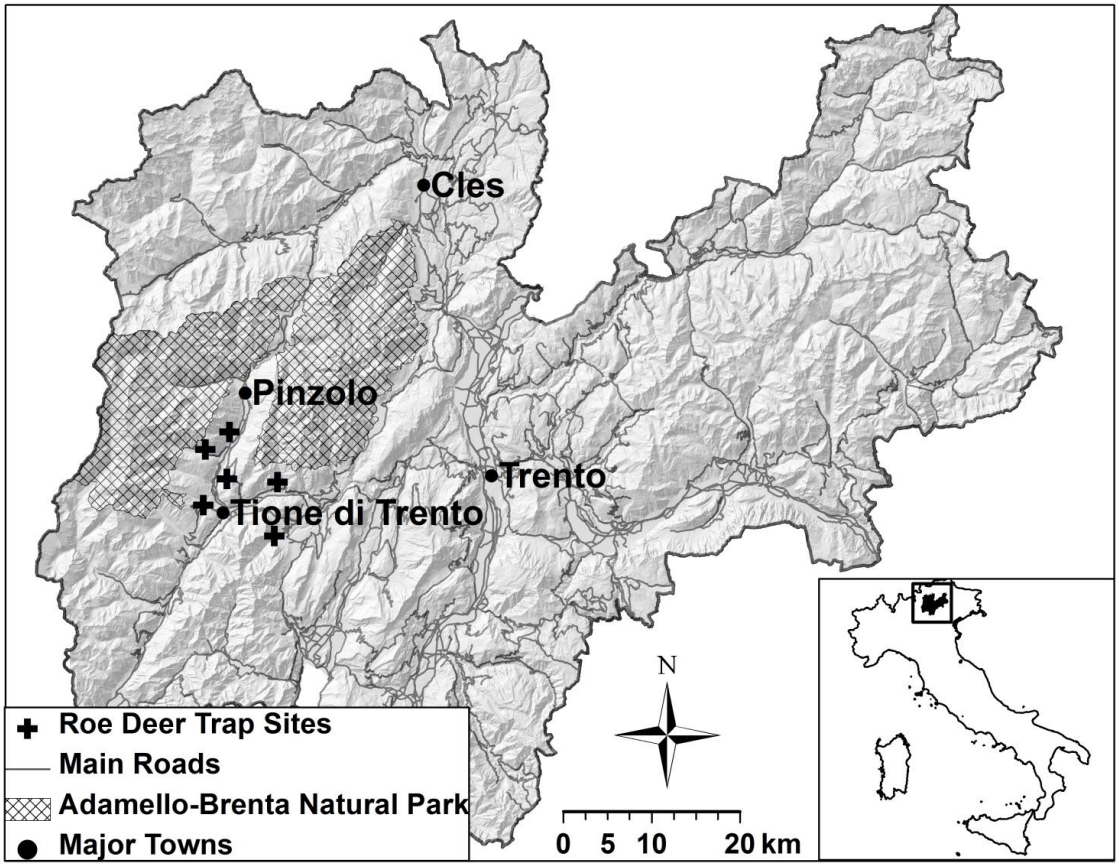


Figure 1. Study area of the summer habitat selection assessment of roe deer. The area is comprised in Trentino (Autonomous Province of Trento), in Italian eastern Alps.

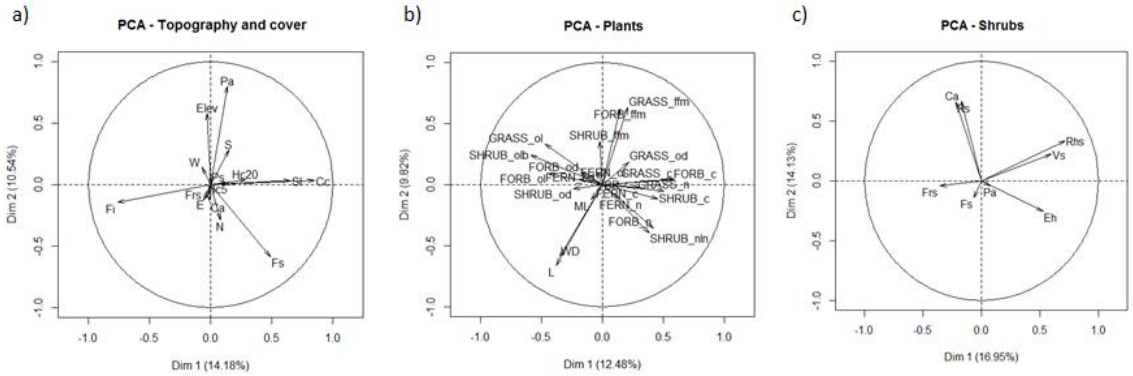


Figure 2. a) PCA biplot for all covariates of the "topography and cover" dataset; Ca = *Corylus avellana*, Cc = canopy cover, E = east, Elev = elevation, Fs = *Fagus sylvatica*, Fi = field, Frs = *Fraxinus* spp., Hc5 = hiding cover at 5 m, Hc20 = hiding cover at 20 m, N = north, Pa = *Picea abies*, Ps = *Pinus sylvestris*, S = south, Sl = slope, W = west; b) PCA biplot for all covariates of the "plants" dataset; BR = bare and rocks, c = cured, ffm = flowering/fruiting/mature, L = litter, ML = mosses and lichens, n = newlu emergent, nln = newly emergent/old alive with new leaves, ol = old alive, olb = old alive/old alive with buds, od = old dead, WD = woody debris; c) PCA biplot for species covariates of the "shrubs" dataset; Ca = *Corylus avellana*, Eh = *Erica herbacea*, Fs = *Fagus sylvatica*, Frs = *Fraxinus* spp., Pa= *Picea abies*, Rs = *Rubus* spp., Rhs = *Rhododendron* spp., Vs = *Vaccinium* spp. In all cases, the proportion of variance explained by the first (horizontal) and second (vertical) canonical dimension is reported.

Appendix A

Table A1 Habitat covariates sampled by the used and available locations along the movement trajectories of 14 roe deer equipped with GPS telemetry collars. Habitat covariates were sampled during the spring and summer seasons 2013 in the eastern part of the Autonomous Province of Trento, Italy.

Covariate (Scale)	**Spatial Unit**	**Type**	**Covariate Description**
Topography (Macro-habitat)	Location point		
Aspect		Categorical	Eight classes (north, north-east, north-west, south, south-east, south-west, east, west)
Slope		Continuous	Ground downward/upward inclination; degrees (0-50°)
Elevation		Continuous	Altitude a.s.l. (above sea level); meters (457-1916 m)
Habitat type (Macro-habitat)	Grid cell (approx. 50m surrounding)	Categorical	Dominant tree/shrub species or general feature (e.g., field) of sampling locations
Cover (Macro-habitat)	Grid cell (approx. 50m surrounding)		
Canopy cover		Continuous	Mean number of Lemmon's densiometer squares covered by tree crowns against open sky in north, south, east and west (0-24 squares)
Hiding cover at 5 meters		Continuous	Number of covered squares in a cover board at a randomly chosen distance of 5 m from the sampling locations (0-30 squares)
Hiding cover at 20 meters		Continuous	Number of covered squares in a cover board at a randomly chosen distance of 20 m from the sampling locations (0-30 squares)
Vegetation composition (Micro-habitat)	Sampling quadrats ($2m^2$)		
Forbs		Continuous	% of 2 $1m^2$ sampling frames covered by forbs
Shrubs		Continuous	% of 2 $1m^2$ sampling frames covered by shrubs (all plant species with a woody stem and a diameter < 5 cm); from 0 to 1.5 m above soil level

Grasses/sedges		Continuous	% of 2 $1m^2$ sampling frames covered by grasses/sedges
Ferns		Continuous	% of 2 $1m^2$ sampling frames covered by ferns
Ground-layer (Micro-habitat)	Sampling quadrats ($2m^2$)		
Bare/rocks		Continuous	% of 2 $1m^2$ sampling frames covered by bare and rocks
Woody debris		Continuous	% of 2 $1m^2$ sampling frames covered by woody debris
Mosses/lichens		Continuous	% of 2 $1m^2$ sampling frames covered by mosses and lichens
Litter		Continuous	% of 2 $1m^2$ sampling frames covered by litter (dead leaves, needles and cones)
Shrub composition (Micro-habitat)	Sampling quarter circle ($7m^2$)		
Shrub species		Categorical	Shrub species present within a 3 m radius quarter circle from the lower left corner of the first sampling frame
Vegetation/shrub phenology (Micro-habitat)	Sampling subunit (quadrat or quarter circle)		
Old alive		Continuous	% of old alive plants
Newly emergent		Continuous	% of newly emergent plants
Old alive with new leaves		Continuous	% of shrubs with new leaves
Old alive with buds		Continuous	% of shrubs with buds
Flowering		Continuous	% of plants with flowers
Fruiting		Continuous	% of plants with fruits
Mature		Continuous	% of plants with both flowers and fruits
Cured		Continuous	% of plants dead the current year
Old dead		Continuous	% of plants dead the previous year

Table A2a AIC, ΔAIC and AIC weights for the top models (ΔAIC<2) for 'topography and cover'; models were obtained using conventional logistic regression; Ca = *Corylus avellana*, Cc = canopy cover, Elev = elevation, Frs = *Fraxinus* spp., Hc20 = hiding cover at 20 m.

Ranked models	**AIC**	**ΔAIC**	**AICw**
Model 1: Used/Avail ~ Ca + Cc + Frs + Hc20	782.64	0	0.45
Model 2: Used/Avail ~ Ca + Cc + Frs + Hc20 + Elev	783.49	0.85	0.29
Model 3: Used/Avail ~ Ca + Cc + Frs	783.78	1.14	0.25

Table A2b AIC, ΔAIC and AIC weights for the top models (ΔAIC<2) for 'topography and cover'; models were obtained using conditional logistic regression; habitat covariates specifications as in Table A2a.

Ranked models	**AIC**	**ΔAIC**	**AICw**
Model 1: Used/Avail ~ Ca + Cc + Frs + Hc20	356.44	0	0.49
Model 2: Used/Avail ~ Ca + Cc + Frs + Hc20 + Elev	358.64	1.24	0.27
Model 5: Used/Avail ~ Cc + Cc + Frs	362.90	1.44	0.24

Table A3a AIC, ΔAIC and AIC weights for the top models (ΔAIC<2) for 'plants'; models were obtained using conventional logistic regression; n = new, ffm = flowering/fruiting/mature.

Ranked models	**AIC**	**ΔAIC**	**AICw**
Model 1: Used/Avail ~ shrub_nln + shrub_ffm	803.73	0	0.22
Model 2: Used/Avail ~ grass_n + shrub_nln + shrub_ffm	804.16	0.44	0.17
Model 3: Used/Avail ~ forb_ffm + shrub_nln + shrub_ffm	804.81	1.08	0.13
Model 4: Used/Avail ~ shrub_nln	804.94	1.22	0.12
Model 5: Used/Avail ~ forb_ffm + grass_n + shrub_nln + shrub_ffm	805.00	1.27	0.11
Model 6: Used/Avail ~ grass_n + shrub_nln	805.56	1.83	0.09
Model 7: Used/Avail ~ grass_ffm + shrub_nln + shrub_ffm	805.59	1.86	0.09
Model 8: Used/Avail ~ forb_n + shrub_nln + shrub_ffm	805.72	2.00	0.08

Table A3b AIC, ΔAIC and AIC weights for the top models (ΔAIC<2) for 'plants'; models were obtained using conditional logistic regression; habitat covariates specifications as in Table A3a.

Ranked models	**AIC**	**ΔAIC**	**AIC w**
Model 1: Used/Avail ~ grass_nln + shrub_nln + shrub_ffm	393.43	0	0.45
Model 2: Used/Avail ~ forb_ffm + grass_n + shrub_nln + shrub_ffm	393.89	0.46	0.35
Model 8: Used/Avail ~ grass_n + shrub_nln	395.02	1.59	0.20

Table A4a AIC, ΔAIC and AIC weights for the top models (ΔAIC<2) for 'shrub'; models were obtained using conventional logistic regression; Frs = *Fraxinus* spp., G1 = group 1 (*Corylus avellana* + *Rubus* spp.), G2 = group 2 (*Erica herbacea* + *Rhododendron* spp. + *Vaccinium* spp), nln = new/old alive with new leaves, olb = old alive/old alive with buds.

Ranked models	**AIC**	**ΔAIC**	**AICw**
Model 1: Used/Avail ~ Frs_nln + G2_nln + G2_olb	784.86	0.00	0.41
Model 2: Used/Avail ~ Frs_nln + Frs_olb + G2_nln + G2_olb	786.19	1.33	0.21
Model 3: Used/Avail ~ Frs_nln + G1_nln + G2_nln + G2_olb	786.35	1.49	0.19
Model 4: Used/Avail ~ Frs_nln + G1_olb + G2_nln + G2_olb	786.40	1.54	0.19

Table A4b AIC, ΔAIC and AIC weights for the top models (ΔAIC<2) for 'shrub'; models were obtained using conditional logistic regression; habitat covariates specifications as in Table A4a.

Ranked models	**AIC**	**ΔAIC**	**AICw**
Model 1: Used/Avail ~ Frs_nln + G2_nln + G2_olb	375.71	0	0.44
Model 2: Used/Avail ~ Frs_nln + Frs_olb + G2_nln + G2_olb	377.28	1.57	0.20
Model 3: Used/Avail ~ Frs_nln + G1_nln + G2_nln + G2_olb	377.36	1.65	0.19
Model 4: Used/Avail ~ Frs_nln + G1_olb + G2_nln + G2_olb	377.63	1.92	0.17